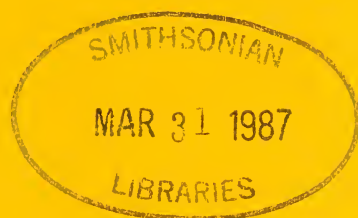# Quaestiones

Entomologicae

A periodical record of entomological investigations,

published at the Department of Entomology,

University of Alberta, Edmonton, Canada.

CONTENTS

CONTENTS

THE ADULT ARCTOPSYCHIDAE AND HYDROPSYCHIDAE (TRICHOPTERA) OF CANADA AND ADJACENT UNITED STATES

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ABSTRACT

Of the six species of Arctopsychidae here reported from Canada and adjacent States of the United States, three belong to each of Arctopsyche *McLachlan* and Parapsyche *Betten*. Of 72 species of Hydropsychidae, 24 belong to Cheumatopsyche *Wallengren*, 42 to Hydropsyche *Pictet*, three to Macrostemum *Kolenati*, and one each to Potamyia *Banks*, Diplectrona *Westwood*, and Aphropsyche *Ross*.

Keys are provided (for males, and females where possible) to genera and species. For each species the habitus is described in some detail, with diagnostic statements for the genitalia. Also included are brief statements about way of life and known distribution. Distributions are mapped, and genitalia are illustrated.

RÉSUMÉ

Soixante et dix-huit espèces d'Arctopsychidae et d'Hydropsychidae (Trichoptera) sont mentionnees pour le Canada et les états frontaliers des États-Unis, representant les genres suivants: Archtopsyche *MeLachlan (3)*, Parapsyche *Betten (Archtopsychidae) (3)*, Cheumatopsyche *Wallengren (24)*, Hydropsyche *Pictet (42)*, Macrostemum *Kolenati (3)*, Potomyia *Banks (1)*, Diplectrona *Westwood (1) et* Aphropsyche *Ross (1)*.

Des clefs d'identification augenre et à l'espèce (pour les mâles, et les femelles lorsque possible) sont presentées par l'auteur. Un habitus ainsi qu' une description diagnostique des pièces génitales sont donnés pour chacune des espèces. Une description résume ce qu' il y a de connu sur l'histoire naturelle et la répartition géographique de ces espèces. Les aires de distributions et les pièces génitales sont largement ilustrées.

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INTRODUCTION

This paper brings together information about all species of Arctopsychidae and Hydropsychidae presently known from Canada, or with the potential to be found in Canada. Consequently, all species of the two families recorded from contiguous States of the United States, but not yet from Canada, are also included here.

The Hydropsychidae is one of the larger families of Trichoptera, world-wide, with 72 species recorded here. These species are distributed among three subfamilies and six genera. The Arctopsychidae, on the other hand, is a small family confined to the Holarctic region and its fringes in south Asia. There are six species recorded here.

Characterisations of supra-specific taxa are abridged from Schmid (1980).

The key to genera is translated from Schmid (1980). For a key to genera of larvae, Wiggins (1977) should be consulted. Keys to species are original, with the exception of that to *Cheumatopsyche* which is partially adapted from Gordon (1974). These keys make fullest possible use of the illustrations, and have been kept as simple as possible: use of more than two characters per couplet has been avoided where possible; for most couplets, only one character is used.

In the text for each species a general habitus description is presented in some detail. This is based on the male, with mention of the female only when she is significantly different. Regarding genitalia, a diagnostic statement only is presented, which makes reference to those characters which will ensure correct recognition of a species in conjunction with the illustrations. The male and female (where known) genitalia of each species are fully illustrated. Notes about way of life and known distribution (with maps) complete the presentation for each species.

Within subfamilies the genera are presented in alphabetical order. Within the genera the species are also presented in alphabetical order, except where the genus has been subdivided to species groups and subgroups, when the alphabetical ordering is used only within the lowest grouping. This latter arrangement is used in *Cheumatopsyche* and *Hydropsyche*. In *Cheumatopsyche* I use the infra-generic group names of Gordon (1974). In *Hydropsyche* I use a numbering system for the groups, and a letter designation for the subgroups.

At the beginning of each species treatment (as also for the treatment of each genus, subfamily, and family) a brief synopsis of the synonymy attaching to that taxon is presented, with citations of the more important papers relevant to the history of the taxon. For a complete listing of literature for each taxon, up to 1961 inclusive, Fischer (1963; 1972) should be consulted.

Statements about colour are based on alcohol-preserved material. With such material, fading may occur over time, and wing and body hairs may be lost. Wing colouration, therefore, is based on membrane colour. This is the normal situation with fluid-preserved material, which

is usual in bulk collecting especially.

Species recognition in adults is based almost entirely on male and female genitalia. In the males I follow Snodgrass (1957:35) in considering the aedeagus to be the entire evertible assemblage located between the claspers (inferior appendages). I also prefer to use the term *clasper*, rather than *inferior appendage*, as it has the merit of brevity and of describing the apparent function of the appendage in question. The abdominal segments are referred to by use of roman numerals, counting from the abdomen-thorax junction.

From the illustrations of genitalia I omit setae or hairs except in instances where they may be of use in identification of a given species; otherwise they simply clutter the drawing and obscure other features. The genitalia of many species are, however, well invested with setae or hairs.

One final point to note, regarding descriptions or characterisations, is the use of the singular and plural. Several components of the genitalia are paired but, in certain views only one member of a pair is visible. When one member only is visible the singular is used. When both are visible, the plural is generally used. Reference to the wings and legs is normally on the basis of one member of each pair.

TECHNIQUES

Refer to Nimmo (1971) for details about collection, preservation, and preparation of material for examination.

GEOGRAPHICAL DISTRIBUTION

A distribution map, or maps, is presented for each species dealt with here. For those species presently known from Canada a detailed map of the Canadian distribution is given. An inset map of North America presents a by state/province overview of the total known distribution in North America. For those species not yet recorded from Canada only the overall North American map is presented.

The State records for the United States portion of the North American maps are derived from the literature. Most of the detailed Canadian records are new to the literature and are derived from examination of museum or newly collected material. Such detailed records as were obtained from the literature are considered to be trustworthy and no distinction is made on the maps.

Apart from the transcontinental species the fauna may be divided into those relatively few species known from the Rocky Mountain foothills and west, and the great bulk of species which occur east of these foothills. A very few of these last are apparently restricted to the Great Plains. The remainder are centred on eastern North America with extensions to the north-west, to the north-east, and to the south, or combinations of these. Some species appear to be confined to the environs of the Appalachians, or to the southern fringes of the Great Lakes, with or without extensions southward along the valley of the Mississippi River. Many species are still too poorly known for useful speculation regarding their distribution patterns.

Other than records of a few species from northern Québec, these two families appear to be limited northwards by the tree line.

A single, transcontinental, species is holarctic in total distribution, being known from Eurasia as far west as northern Europe.

NOTE ADDED IN PRESS

Schefter, Wiggins, & Unzicker (1986) recently synonymized names of two species dealt with here: *Hydropsyche jewetti* Denning (=*H. cockerelli* Banks); and *Hydropsyche riola* Denning (=*H. alhedra* Ross). Similarly, Schefter & Unzicker (1984) synonymised *Hydropsyche bifida* Banks with *H. morosa* Hagen.

These synonymizations may be correct; indeed I am inclined to accept that they are. However, in course of preparation of this paper, I encountered no material which might support the above synonymizations, and prefer, for present purposes, to leave the text as originally written. Thus, I have inserted guiding notes, in the appropriate parts of the text, relating to this particular note.

THE FAMILY ARCTOPSYCHIDAE MARTYNOV

Arctopsychidae Martynov, 1924:25; Schmid, 1968:4; Schmid, 1980:51.
Arctopsychinae (Hydropsychidae); Milne, 1940:13, 19; Flint, 1961:5; Ross, 1956:10; Wiggins, 1977:93.

Description.— Females distinctly larger, more robust than males. Ocelli absent. Maxillary palpi of five articles; with basal two articles very short, sub-equal; article four slightly shorter than article three; article five long, flagellate. Antennae thickened, especially in male; with short, globular scape. Spurs large; spur formula 2,4,4. Fore- and hind-wings (Fig. 2) virtually identical in individuals and between sexes; nearly oval in outline but hind-wings with anal edge evenly rounded. Venation similar in the two genera dealt with here: fI-V present in fore-wings, fI-III and fV present in hind-wings. Fore-wings with discoidal, median, and thyridial cells closed; thyridial cell especially long; cross-veins C-Sc, Sc-R1, and R1-R2+3 present; Cu2 terminated on A rather than on anal edge of wing; postcostal cell very large. Hind-wing with cross-veins C-Sc and Sc-R1 present; with four separate anal veins.

Genitalia. Male. (Fig. 7–9, 25–28). Segment IX well developed dorsally. Preanal appendages free or fused to segment X. Intermediate appendages also free or fused to each other. Claspers (inferior appendages) large or small, bipartite. Aedeagus large, located high in the abdomen composed of tubular phallotheca with invaginated small, membranous, erectile endotheca.

Genitalia. Female (Fig. 11–12, 29–30). Segments X and XI short. Tergite VIII very large; lateral edges produced quite far ventrad. Sternite VIII correspondingly reduced, with posterior edge terminated in two large lobes. Segment IX absent. Segment X enclosed by lobes of Sternite VIII, short, simple, without clasper receptacles; postero-dorsal edge with two small tubercles, each with slender brush of very long hairs. Segment X with large, postero-ventral, membranous vulval scale. Ano-vaginal opening on posterior end of segment X.

The Arctopsychidae are very closely related to the Hydropsychidae, and some authors regard it as a subfamily of the Hydropsychidae (Wiggins, 1977). Based on Schmid (1968), and taking account of Smith (1968), the Arctopsychidae encompass two known genera and a minimum of 43 species worldwide. The family is oriental and holarctic in overall distribution, with most species concentrated in a zone extending from the Himalaya to Japan. Eleven species (one of which is holarctic) are currently recognised in North America, with five known to occur in Canada and a sixth possibly to be found here. Both genera occur in Canada, with three and two (three?) species of each represented.

Key to genera of Arctopsychidae of Canada

1a   Eyes glabrous. Male genitalia protuberant, not recessed into segment VIII. Tibia and tarsus of female middle leg flattened, enlarged . . . .*Arctopsyche* McLachlan, p. 5

1b   Eyes hairy. Male genitalia barely protuberant, recessed into segment VIII. Tibia   and   tarsus   of   female   middle   leg   not   flattened,   not enlarged . . . . *Parapsyche* Betten, p. 14

Genus *Arctopsyche* McLachlan
Maps 1–3; Fig. 2, 7–24

Arctopsyche McLachlan, 1868:300; Betten, 1934:179, 180; Milne, 1936:65; Flint, 1961:6; Schmid, 1968:21, 29, 32; Wiggins, 1977:98; Schmid, 1980:52.

Description.— Eyes glabrous. Third article of maxillary palpi twice as long as wide; not much longer than fourth. Spur formula 2,4,4. Tibia and tarsus of female middle leg enlarged, flattened, fringed with hairs. Discoidal cell of fore- and hind-wings (Fig. 2), and median cell of fore-wing small.

Genitalia. Male. (Fig. 7–10, 13–16, 19–22). Segment IX nearly as large as VIII, not recessed within VIII. Preanal appendages free (Fig. 7, 9); long, narrow, rounded. Intermediate appendages (Fig. 7, 9) stout, long blades; single or paired; simple or with dentitions. Segment X entirely membranous, either very short or as long slender tube (Fig. 19, 20) depending on species group. Claspers (inferior appendages) (Fig. 7, 8) with two articles, reduced in size, complex; basal article massive, with dorsal lobe or spine and two or three ventral spines; distal article small, inserted between spines of basal article. Aedeagus (Fig. 10) large, stout, with recurved internal phallotremal sclerite.

Genitalia. Female. (Fig. 11–12, 17–18, 23–24). Postero-dorsal margin of segment X with inconspicuous flange (Fig. 11). Segment XI developed basad.

In Canada *Arctopsyche* is represented by two species; one of these (*A. ladogensis*) is holarctic in distribution, being recorded in boreal regions from northwestern Europe to Newfoundland. A third species (*A. irrorata*) is presently known only from the southeastern United States but may eventually be recognised from eastern Canada. *A. grandis* is primarily a western montane species, but has been recorded from northwestern Québec.

Key to known or potential species of *Arctopsyche* McLachlan of Canada

Arctopsyche grandis Banks
Map 1; Fig. 7–12

Arctopsyche grandis Banks, 1900:258; Milne, 1936:66 (*A. phryganoides* as synonym); Ross, 1938c:14; Schmid, 1968:54; Smith, 1968:109 (*A. inermis* as synonym); Wiggins, 1977:99.
Arctopsyche phryganoides Banks, 1918:21; Milne, 1936:66 (as synonym of *A. grandis*).
Arctopsyche inermis Banks, 1943:368; Smith, 1968:109 (as synonym of *A. grandis*); Schmid, 1968:54.

Description.— Male fore-wing length 12.56 mm; pale grey-brown with uniform faint irroration except for coalescence of pale areas along costal edge; female irroration more evident. Hind-wing faintly tinted golden brown; grey-brown in female. Antennae brown-cream; basal 19 flagellar annuli of male each with simple black bands; 17–18 in female. Vertex dark brown. Spurs brown; lateral member of middle leg pairs notably shorter than mesal companions. Thorax dark brown, to pale yellow-brown laterally. Legs pale brownish yellow.

Genitalia. Male. (Fig. 7–9). (Specimen from Wildhorse camp, Ya Ha Tinda Ranch road, Alberta). Males distinguished by apparent lack of segment X (Fig. 7, 9); by dorsal lobe of clasper basal article broad in lateral aspect, angled posterad (Fig. 7); and by ventral lobe of clasper basal article terminated in several acuminate teeth in ventral aspect (Fig. 8).

Genitalia. Female. (Fig. 11-12). (Specimen from Wildhorse camp, Ya Ha Tinda Ranch road, Alberta). Females distinguished by complexity of vulval scale in ventral aspect; scale with semi-circular posterior edge (Fig. 12) terminated laterally by lateral processes; anterad of processes scale markedly constricted and anterad of constriction scale abruptly expanded to greater width.

Biology.— British Columbia and Alberta records give flight season extremes of June 6 to August 27, and May 26 to August 12 respectively, with definite peak indicated for July as a whole. Smith's (1968) records from Idaho conform to much the same pattern. He adds that the commonest life stages in winter were mature larvae, with pupation occurring from April to May. He concludes that this species has a two-year life cycle. My records indicate that adults emerge from the largest mountain and foothill rivers, from smaller, riffled foothill streams, from turbulent mountain streams, and from all intermediate types of flowing water in mountain and foothill country. Adults have also been collected from clear, riffled, cool streams in low-altitude terrain of little relief. Larvae appear to be, ecologically, very diverse or tolerant. Wallace (1975a) presents information in support of the predaceous nature of larvae of *Arctopsyche*. Mecom (1972) contends that *A. grandis* larvae are carnivorous in summer months, but primarily phytophagous, diatom feeders, or detritovores at other times.

Distribution.— Recorded from the Yukon and western Northwest Territories in Canada, to California and New Mexico in the United States, with one record from northwestern Québec (Map 1) in Canada; excepting the Québec record, this species appears to be confined to the Cordillera west of the Great Plains.

<center>

Arctopsyche irrorata Banks
Map 2; Fig. 13–18

</center>

Arctopsyche irrorata Banks, 1905b:217; Milne, 1936:66.

Description.— Male fore-wing length 14.43 mm; medium grey-brown; randomly irrorate throughout, except more regular alternate hyaline and coloured patches along costal edge and posterad as far as Rs. Hind-wing tinted grey-brown (very pale). Antennae pale orange-brown; each annulus with deep chocolate-brown band on dorsal and lateral surfaces, at right-angles to axis of annulus; scape with rectangular patch of dark brown laterally. Vertex pale orange-brown to red-brown. Spurs red-brown; lateral member of each pair shorter than mesal companions. Thorax deep red-brown dorsally, pale straw to cream laterally. Legs pale red-brown. Female overall darker than male.

Genitalia. Male. (Fig. 13–16). (Specimen from Citico Ck, Monroe Co., Tennessee, USA). Males distinguished by each member of intermediate appendage pair bifid (Fig. 13, 15); by apparent lack of segment X; by ventral lobe of clasper single, not subdivided (Fig. 14), with distal hook turned dorsad in lateral aspect (Fig. 13); and by dorsal lobe of clasper directed dorsad, irregular in outline.

Genitalia. Female. (Fig. 17–18). (Specimen from Citico Ck, Monroe Co., Tennessee, USA). Females distinguished by vulval scale fairly regular in ventral outline (Fig. 18), straight-edged laterally, with central portion slightly raised, tapered posterad, and with semi-circular membranous lobe on distal edge.

Biology.— Flint (1961) records small larvae in early summer, mature larvae in fall, and adult flight season as late May and June. Overwintering is by mature larvae. He adds that larvae live in fairly large streams up to 25 m wide, and 1 m deep; the water is clear, cold, with gravel and boulder substrate. He also records abundance of larvae in shallow water falling rapidly over bedrock. Both animal and plant material are consumed, with animal matter predominating. Wallace (1975a) provides full details about retreat and net structure, and

seasonal feeding habits.

Distribution.— To date this species is recorded definitely only from Tennessee, and North & South Carolina (Map 2). Ross (1944) records the species from 'eastern States and eastern Canada', hence its inclusion here. But as, in the same sentence, he also includes *A. ladogensis*, this 'record' may simply result from imprecise wording. More definite records could not be found to substantiate Ross' statement.

Arctopsyche ladogensis (Kolenati)
Map 3; Fig. 19–24

Aphelocheira ladogensis Kolenati, 1859:145, 147, 165, 183, 201.
Arctopsyche ladogensis; McLachlan, 1868:301; Milne, 1936:66, 67; Schmid, 1968:56.
Arctopsyche ladogensis form. *ramosa* McLachlan, 1878:379; Milne, 1936:67.
Arctopsyche ladogensis form. *obesa* McLachlan, 1868:301; Milne, 1936:67.

Description.— Male fore-wing length 11.23 mm; light purplish brown, no pattern evident. Hind-wing palely tinted brown. Antennae pale yellow-brown; basal 19 flagellar annuli with at least trace of darker encircling band; 14 in female. Vertex deep red-brown. Spurs brown; lateral member of middle leg pairs markedly shorter than mesal companions. Thorax very deep purplish brown-black, to paler, mottled red-brown laterally. Legs brown, to straw distally.

Genitalia. Male. (Fig. 19–22). (Specimen from House R., Hwy 63, S of Ft McMurray, Alberta). Males distinguished by segment X prominent (Fig. 19, 20); by much smaller clasper with finger-like dorsal lobe accompanied by spine immediately anterad (Fig. 19); and by distinct dorsal spine on distal edge of aedeagus (Fig. 22).

Genitalia. Female. (Fig. 23–24). (Specimen from House R., Hwy 63, S of Ft McMurray, Alberta). Females distinguished by vulval scale simple, tapered, with slight mesal extension of posterior edge (Fig. 24); and by transverse line of darker colour in form of a W in ventral aspect.

Biology.— Flint (1961) records larvae of this species from clear, cold streams of up to 25 m width and 1 m depth, on gravel or boulder beds. Retreat and net are typical for the genus. Mature larvae are recorded in August and May, and are apparently the overwintering stage. Pupation occurs in late May or June. Flight records are for June (Flint, 1961). Records available to me from Canada give a flight season from May 12 to August 18, with the bulk in June and July. I have records, from northwestern Canada, of adults taken adjacent to rivers of 75 m width or more.

Distribution.— In North America this circumboreal species is known from western Alaska to Newfoundland, the northeastern United States, and Michigan (Map 3). From the Map one might conclude that the species is limited northward by tree line.

Map 1. Collection localities for *Arctopsyche grandis* (Banks) in Canada, with known distribution in North America by state or province.

Map 2. Known distribution of *Arctopsyche irrorata* Banks in North America, by state.
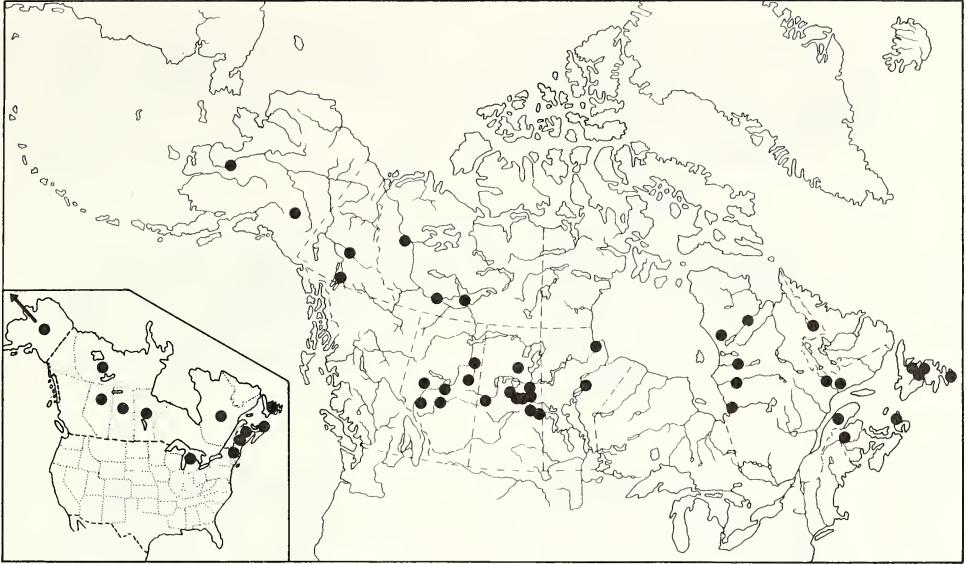
Map 3. Collection localities for *Arctopsyche ladogensis* (Kolenati) in Canada and Alaska, with known distribution in North America by state or province.
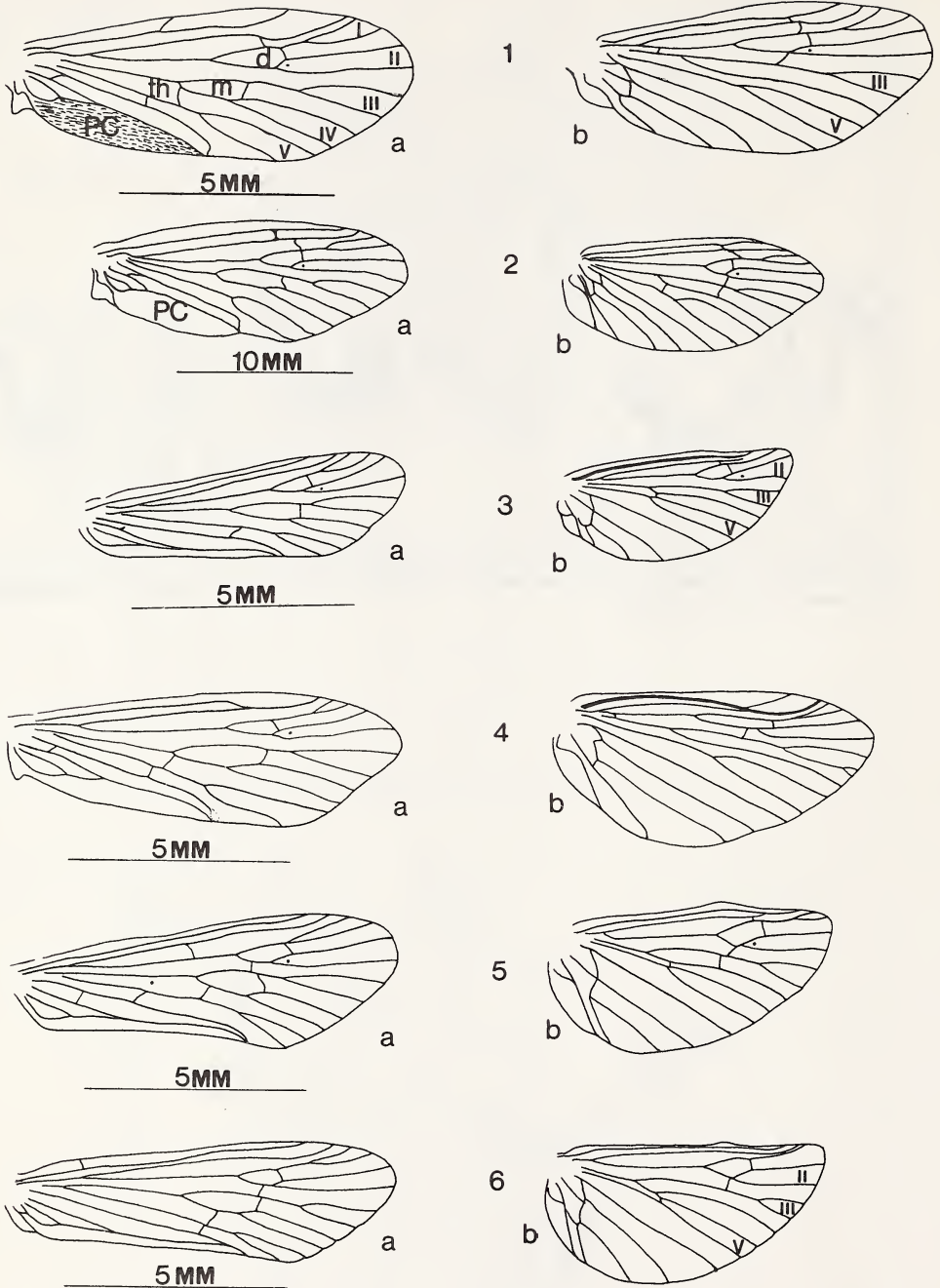
Fig. 1–6. Wing venation, males. 1, *Apropsyche doringa* (Milne). 2, *Arctopsyche irrorata* Banks. 3, *Cheumatopsyche pettiti* (Banks). 4, *Diplectrona modesta* Banks. 5, *Hydropsyche alhedra* Ross. 6, *Potamyia flava* (Hagen). 'a' figures are fore-wings; 'b' are hind-wings. d, discoidal cell; m, median cell; th, thyridial cell; pc, postcostal cell.
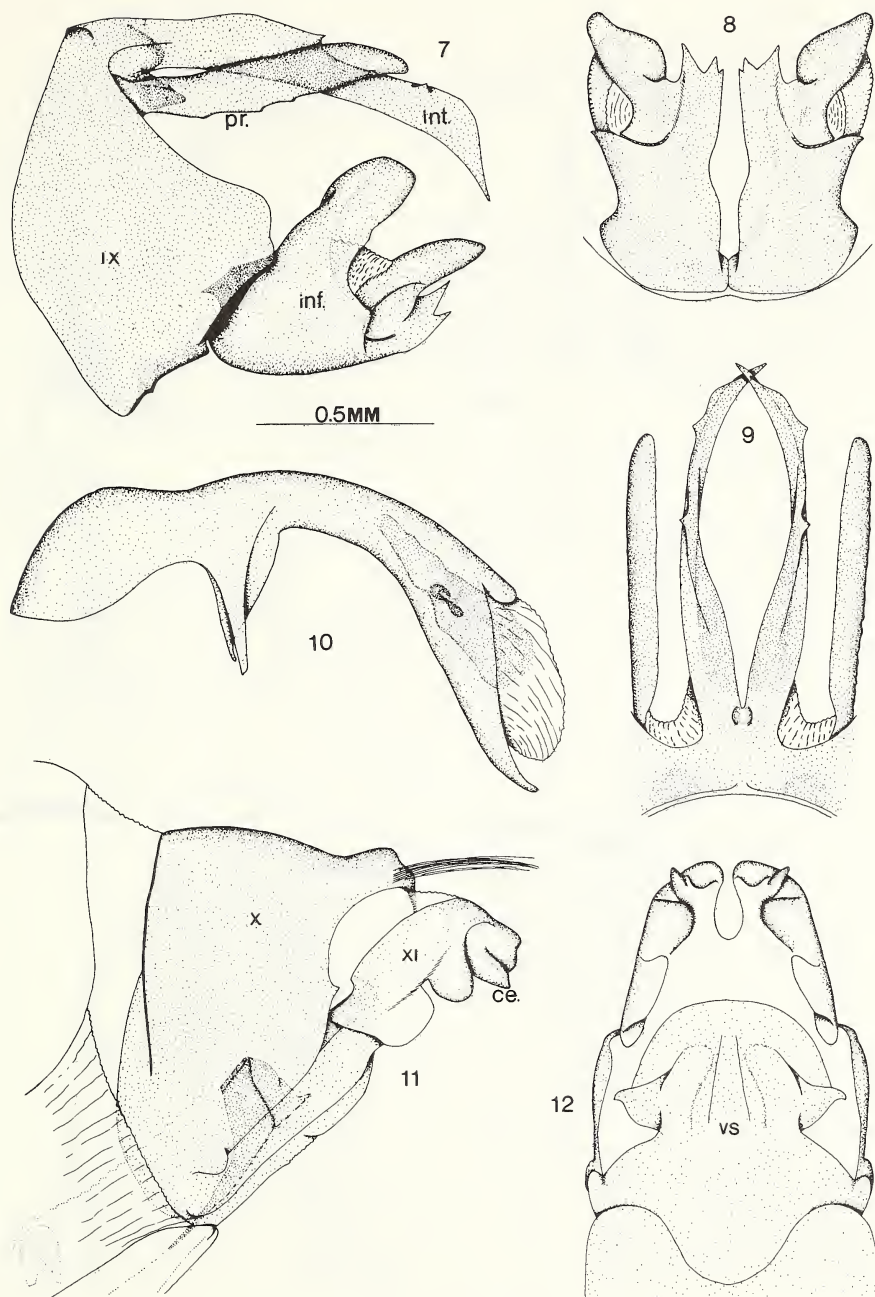
Fig. 7–12, *Arctopsyche grandis* (Banks): 7, genital capsule of male, lateral aspect; 8, claspers of male, ventral aspect; 9, intermediate and preanal appendages of male, dorsal aspect; 10, aedeagus of male, lateral aspect; 11, genital segments of female, lateral aspect; 12, genital segments of female, ventral aspect. inf, inferior appendage (clasper); int, intermediate appendage; pr, preanal appendage; ce, cercus; vs, vulval scale.
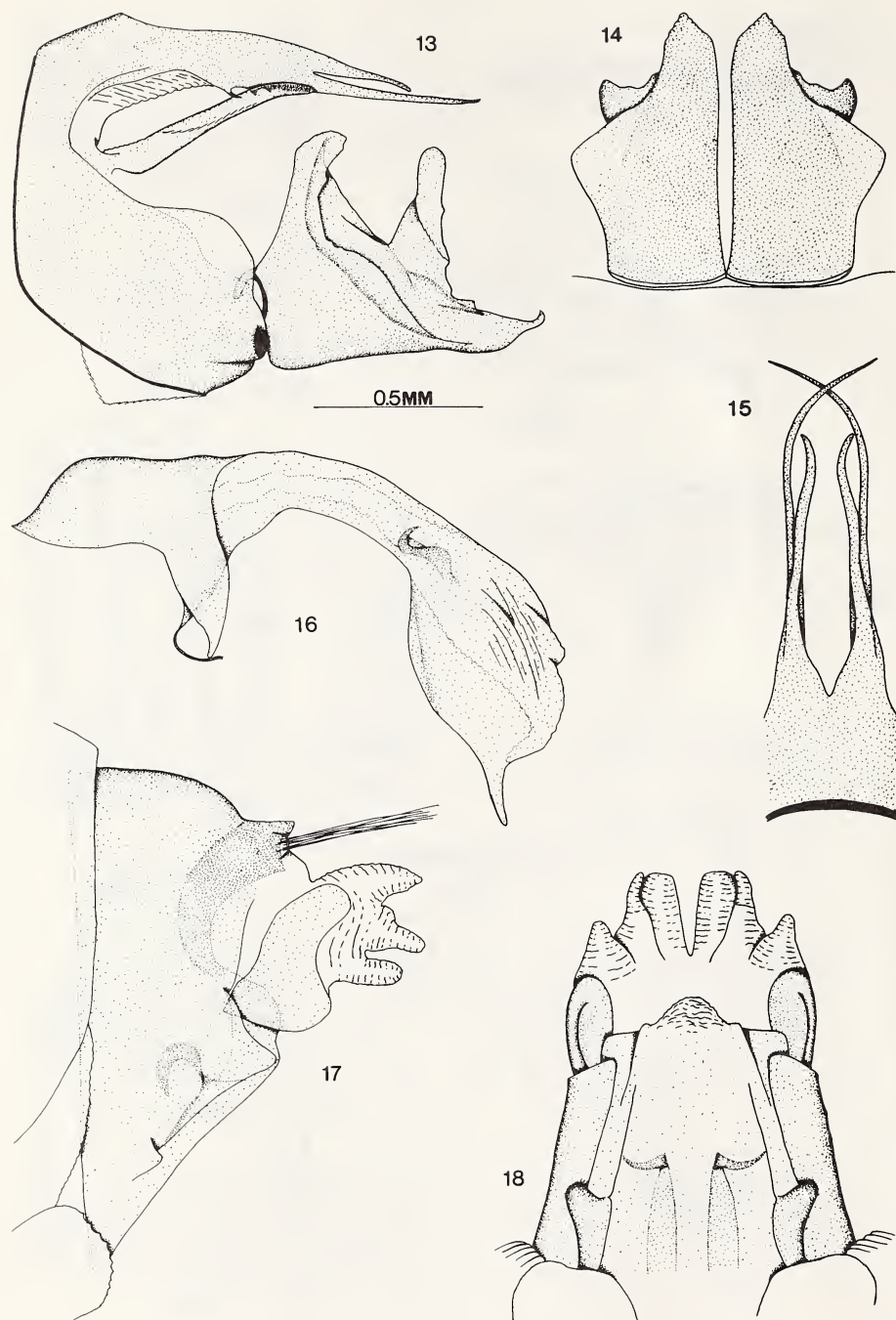
Fig. 13–18, *Arctopsyche irrorata* Banks: 13, genital capsule of male, lateral aspect; 14, claspers of male, ventral aspect; 15, intermediate appendages of male, dorsal aspect; 16, aedeagus of male, lateral aspect; 17, genital segments of female, lateral aspect; 18, genital segments of female, ventral aspect.
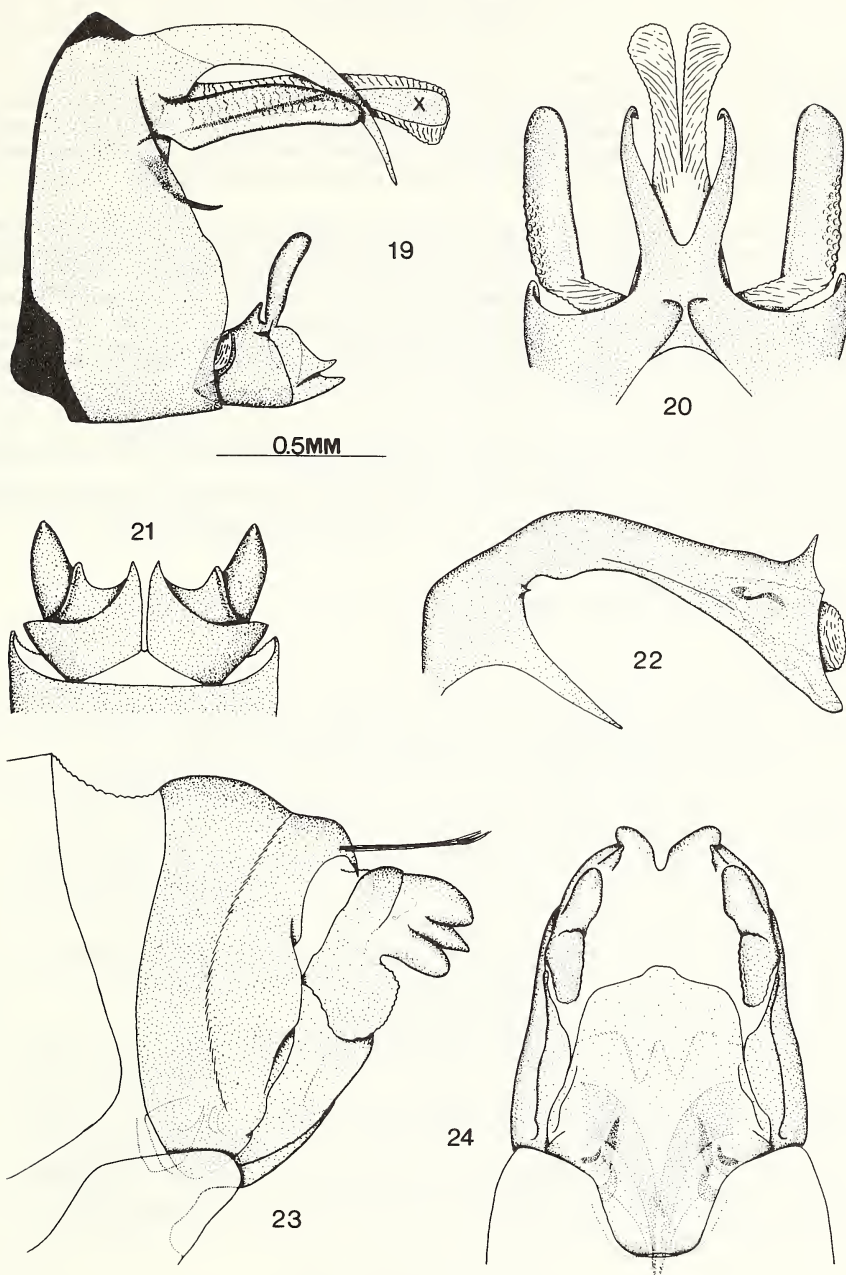
Fig. 19–24, *Arctopsyche ladogensis* (Kolenati): 19, genital capsule of male, lateral aspect; 20, genital capsule of male, dorsal aspect; 21, claspers of male, ventral aspect; 22, aedeagus of male, lateral aspect; 23, genital segments of female, lateral aspect; 24, genital segments of female, ventral aspect.

Genus *Parapsyche* Betten
Maps 4–6; Fig. 25–43

Parapsyche Betten, 1934:179, 181; Schmid, 1968:26, 31, 60; Wiggins, 1977:114; Schmid, 1980:53.

   Description.— Eyes densely clothed with long hairs. Palpi little longer than in *Arctopsyche*. Third article of maxillary palpi at least three times longer than wide; with noticeable bulge on mesal face. Spur formula 2,4,4. Tibia and tarsus of female middle leg not flattened, not enlarged, not fringed with hairs. Hind leg femur very long, tarsi reduced, especially in female. Venation identical to that of *Arctopsyche* except discoidal and median cells of fore-wing distinctly longer.

   Genitalia. Male. (Fig. 25–28, 31–35, 38–41). Segment IX rather small; partly recessed into segment VIII; short, with dorsal part prominent due to lower position of intermediate appendages (Fig. 25). Preanal appendages closely blended with base of intermediate appendages apparently little more than scars. Intermediate appendages large, horizontal, slightly sclerotised blades; fused basally (Fig. 26) or throughout most of their length (Fig. 40); connected to aedeagus by two clearly visible internal straps (Fig. 25, 26, 28). Claspers (inferior appendages) large, directed somewhat postero-dorsad (Fig. 25); with two articles. Basal article of clasper large; distal article on apex or middle of basal article; articles partly fused (Fig. 25, 27). Aedeagus with tubular phallotheca, and membranous, erectile endotheca with external, paired phalotremal sclerites curved basad (Fig. 28). Phallotheca surmounted by dorsal lobe, a prolongation of postero-dorsal margin of basal phallocrypt.

   Genitalia. Female. (Fig. 29–30, 36–37, 42–43). Very similar to *Arctopsyche*. Dorso-lateral posterior margin of segment X not flanged (Fig. 29). Segment XI produced less prominently basad.

   In Canada *Parapsyche* is represented by three species, two of which are western cordilleran, and the third eastern, in distribution. The larvae of all three species are known.

Key to species of *Parapsyche* of Canada

1a   Males . . . . / 2
1b   Females 4
2a   (1a) Intermediate appendages, in dorsal aspect (Fig. 26, 33), fused only at base 3
2b   Intermediate appendages fused throughout length (Fig. 40) . . . .
          . . . . *P. elsis* Milne, p. 16
3a   (2a) Dorsal part of segment IX smoothly continuous with main body of
          segment, along posterior edge (Fig. 25). Western cordilleran species (Map
          4) . . . . *P. almota* Ross, p. 14
3b   Dorsal part of segment IX angled sharply posterad from main body of
          segment (Fig. 31). Eastern species (Map 5) . . . . *P. apicalis* (Banks), p. 15
4a   (1b) Segment X slender in lateral aspect, small (Fig. 29, 36). Vulval scale
          medium to large in ventral aspect (Fig. 30, 37) 5
4b   Segment X massive, wide in lateral aspect (Fig. 42). Vulval scale small in
          ventral aspect (Fig. 43) . . . . *P. elsis* Milne, p. 16
5a   (4a) Vulval scale with triangular, membranous tip (Fig. 30). Eastern species
          (Map 5) . . . . *P. apicalis* (Banks), p. 15
5b   Vulval scale with rounded tip, scarcely membranous (Fig. 37). Western
          cordilleran species (Map 4) . . . . *P. almota* Ross, p. 14

Parapsyche almota Ross
Map 4; Fig. 25–30

Parapsyche almota Ross, 1938a:119; Schmid, 1968:106–107, Fig. 84; Smith, 1968:105.
Arctopsyche oregonensis Ling, 1938:65; Ross, 1944:293.

   Description.— Male fore-wing length 9.36 mm; grey-brown, heavily irrorate, with relatively large areas of hyaline membrane. Hind-wing faintly tinted brown. Female fore-wing more faintly irrorate; hind-wing grey-brown. Antennae

brown; about 19 basal flagellar annuli with dark brown band around each. Vertex red-brown; posterior warts pale. Spurs yellow; lateral member of middle leg pairs notably shorter than mesal companions. Thorax deep chocolate-brown to paler, grey-brown laterally. Legs straw-coloured.

Genitalia. Male. (Fig. 25–28). (Specimen from small, turbulent creek, Hwy 12, 12.7 km NE of Lilloet, British Columbia). Males distinguished by dorsal portion of segment IX smoothly continuous with main body of segment along posterior edge, in lateral aspect (Fig. 25); by intermediate appendages curved dorsad; by distal article of clasper short, conical in lateral aspect; and by intermediate appendages fused only at base (Fig. 26).

Genitalia. Female. (Fig. 29–30). (Specimen from small, turbulent creek, Hwy 12, 12.7 km NE of Lilloet, British Columbia). Females distinguished by segment X narrow (Fig. 29); and by vulval scale with distal half membranous, triangular (Fig. 30).

Biology.— Smith (1968) gives the Idaho flight season as April to October; my scanty Canadian records are within this range. Smith also concludes that medium to mature larvae are the overwintering stages; they are found on the small to medium rubble of small, clear creeks and streams. Of my two records from British Columbia one locality was a steep hill stream flowing over and around large boulders; the second stream was very shallow with fine gravel, at the outlet of a swamp.

Distribution.— This species is presently recorded from the Cariboo-Chilcotin district of west-central British Columbia, to Nevada and California (Map 4) and is probably confined to the Cordillera west of the continental divide. In Canada it is known only from western British Columbia in the southern coastal mountains.

<div align="center">

Parapsyche apicalis (Banks)
Map 5; Fig. 31–37

</div>

Arctopsyche apicalis Banks, 1908:266.
Parapsyche apicalis; Betten, 1934:181; Flint, 1961:8; Schmid, 1968:Fig. 108-110; Wiggins, 1977:115.

Description.— Male fore-wing length 8.58 mm; largely uncoloured membrane with scattered fragments of grey-brown. Antennae pale purplish brown with darker ring near distal end of each annulus. Vertex purple-brown, warts paler; red-brown in female. All spur pairs with lateral members shorter than mesal members. Thorax dark purple-brown dorsally; paler laterally, with some red-brown areas. Female thorax red-brown dorsally, to yellow-brown laterally. Legs yellow.

Genitalia. Male. (Fig. 31–35). (Specimen from Fox Point, Cumberland Co., Nova Scotia). Males distinguished by dorsal portion of segment IX sharply angled posterad (Fig. 31), in lateral aspect; by intermediate appendages more or less linear, sloped slightly ventrad; by distal article of clasper prominent, finger-like; and by intermediate appendages fused only at base.

Genitalia. Female. (Fig. 36–37). (Specimen from Baden, Ontario). Females differentiated by segment X narrow (Fig. 36); and by vulval scale broad, rounded distally, with little distal membrane (Fig. 37).

Biology.— Flint (1961) records the larvae as inhabiting cold (below 10°C), spring-fed brooklets only a metre or so wide and, occasionally, in rushing mountain streams several metres wide. The retreat and net are typical for the family. Overwintering is by larvae of several instars. Pupae occur throughout summer. Adults recorded from May 11 to October 1. Flint considers it possible that there are several generations per year, but without definite broods. The above seasonal information is derived from Massachussetts. Records from Canada give a flight season of May 7 to October 12; some agree with Flint's characterisation of the habitat as cold, spring-fed brooks. The remainder, however, indicate that larvae also inhabit warmer, larger streams.

Distribution.— In North America this species is confined to the eastern half of the continent (Map 5), ranging from Newfoundland and Ontario to Wisconsin, Tennessee, and North Carolina. In Canada the species is recorded from St John's, Newfoundland, to Lake Nipigon, Ontario, and south to the Niagara peninsula. An old record from Colorado almost certainly represents a misidentification of *P. almota* before that species was recognized by Ross – the two species are very similar as adults.

Parapsyche elsis Milne
Map 6; Fig. 38–43

Parapsyche elsis Milne, 1936:66, 67; Schmid, 1968:Fig. 111–113; Smith, 1968:107.

Description.— Male fore-wing length 12.4 mm; pale red-brown (grey-brown in female), very heavily irrorate. Hind-wing tinted pale grey-brown on distal third. Antennae brownish cream; each flagellar annulus encircled in distal quarter by brown band. Vertex brownish yellow except antero-mesal warts brown. Spurs brown; lateral member of middle and hind-leg pairs notably shorter than mesal companions. Thorax yellow-brown, to brownish cream laterally. Legs pale yellow-brown.

Genitalia. Male. (Fig. 38–41). (Specimen from Fiddle R., Hwy 16, Jasper National Park, Alberta). Males distinguished by dorsal portion of segment IX inclined posterad at about 45° to remainder of segment (Fig. 38); by intermediate appendages fused throughout length (Fig. 40), more or less linear, horizontal; by clasper with articles almost indistinguishably fused in lateral aspect (Fig. 38), massive, long; by phallotremal sclerites at tip of aedeagus (Fig. 41) small, with fine spines directed basad.

Genitalia. Female. (Fig. 42–43). (Specimen from Fiddle R., Hwy 16, Jasper National Park, Alberta). Females distinguished by massive, wide segment X in lateral aspect (Fig. 42); and by small vulval scale tapered sinuously distad, distal half trapezoidal, membranous (Fig. 43).

Biology.— Smith (1968) suggests that this species has a two-year life cycle. Overwintering is by young or nearly mature larvae; pupation evident in June and July. Larvae found in flowing waters ranging from small, clear creeks, to largest rivers with boulder beds; from hill streams to mountain torrents. Canadian records indicate flight season ranges from June 26 to September 8.

Distribution.— This species is (with one improbable exception) restricted to the western Cordillera of North America (Map 6), ranging from the Yukon and the Mackenzie Mountains of the Northwest Territories of Canada south to California and Utah. In Canada it is recorded generally from the various ranges of the western Cordillera as far north as the Ogilvie Mountains of the Yukon Territory. An isolated occurrence was recorded for North Carolina. Milne and Milne (1938) had only the five type specimens available at that time, to one of which this curious record is attributed. They make no comment on it. It seems to be so improbable that one is inclined to conclude that it is the result of locality mis-labelling of specimens at some earlier date.
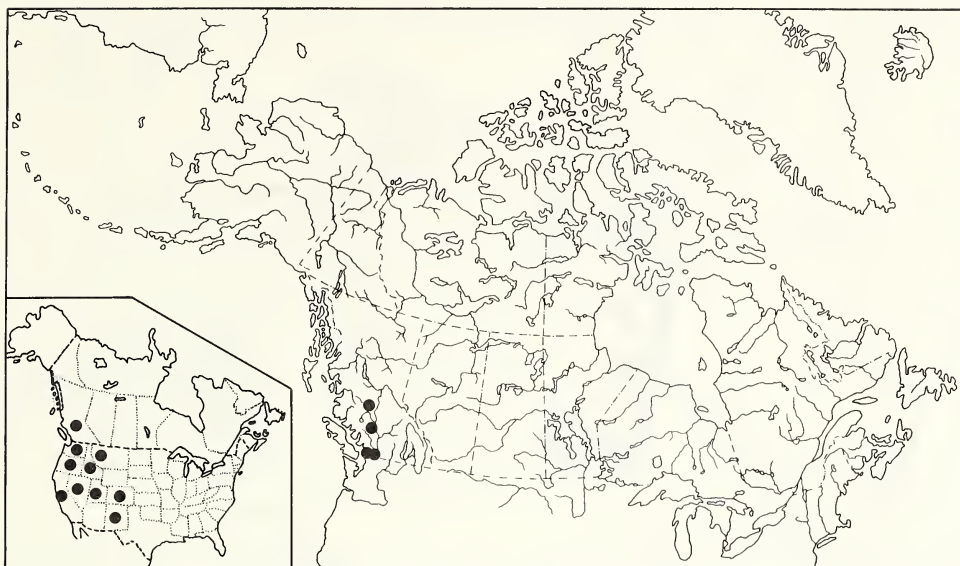
Map 4. Collection localities for *Parapsyche almota* Ross in Canada, with known distribution in North America by state or province.
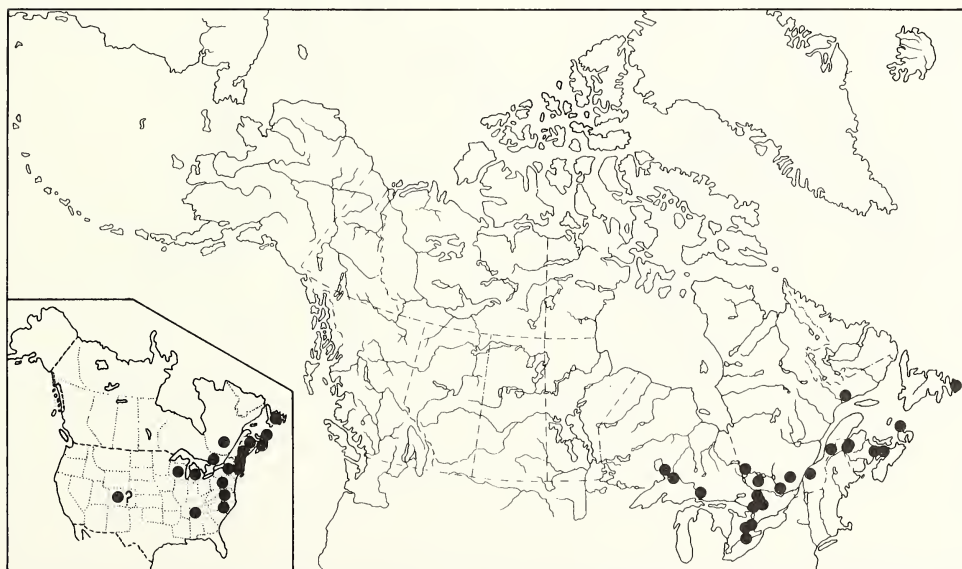
Map 5. Collection localities for *Parapsyche apicalis* (Banks) in Canada, with known distribution in North America by state or province.
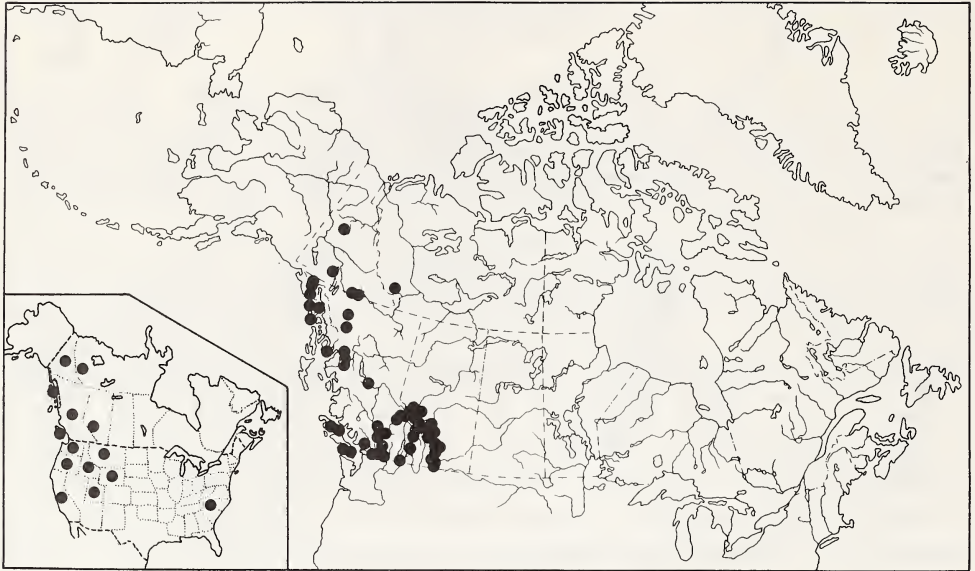
Map 6. Collection localities for *Parapsyche elsis* Milne in Canada and Alaska, with known distribution in North America by state or province.

25

int.

IX

0.5MM

26

27

28

X

XI   ce.

29

VS

30
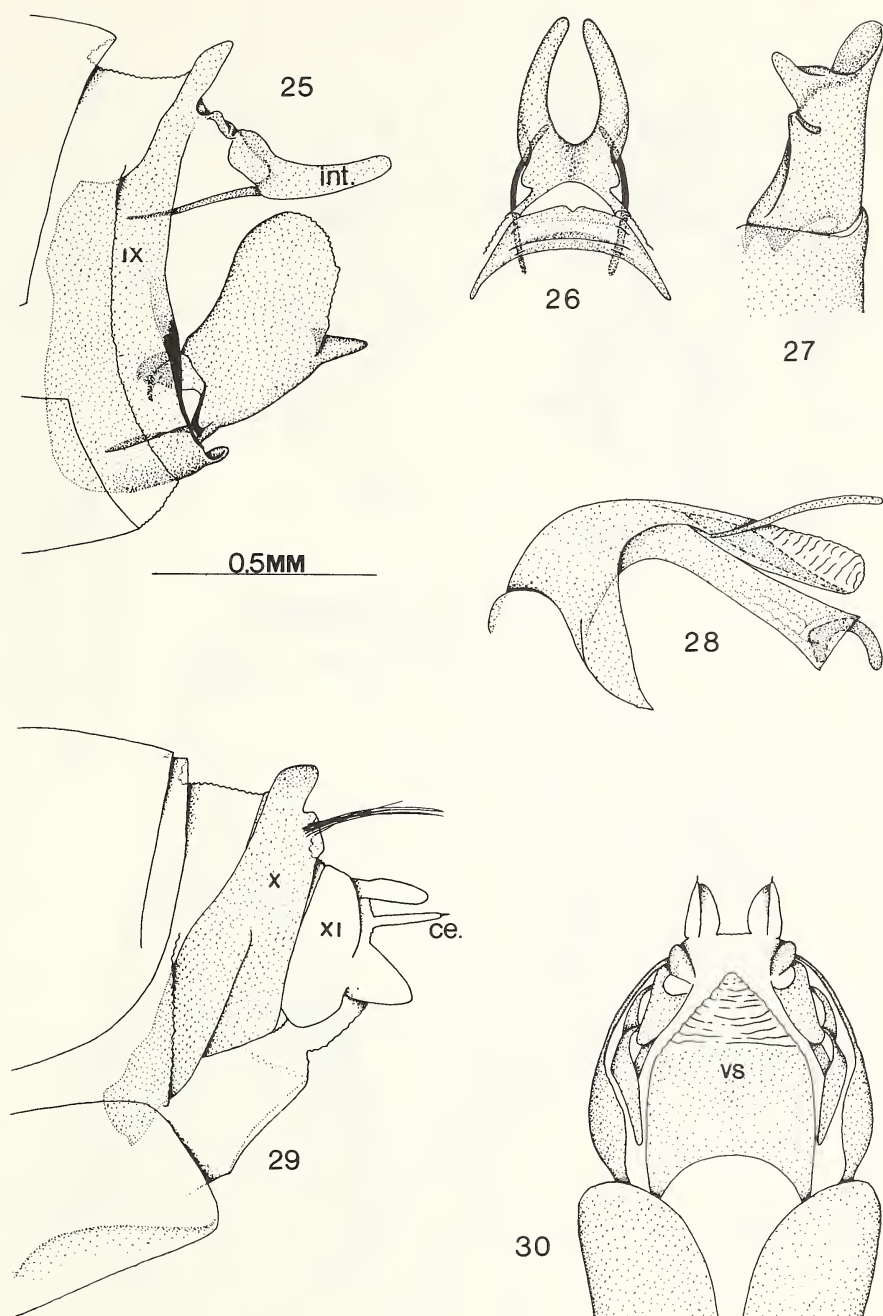
Fig. 25–30, *Parapsyche almota* Ross: 25, genital capsule of male, lateral aspect; 26, genital capsule of male, dorsal aspect; 27, right clasper of male, ventral aspect; 28, aedeagus of male, lateral aspect; 29, genital segments of female, lateral aspect; 30, genital segments of female, ventral aspect. int, intermediate appendage; ce, cercus; vs, vulval scale.
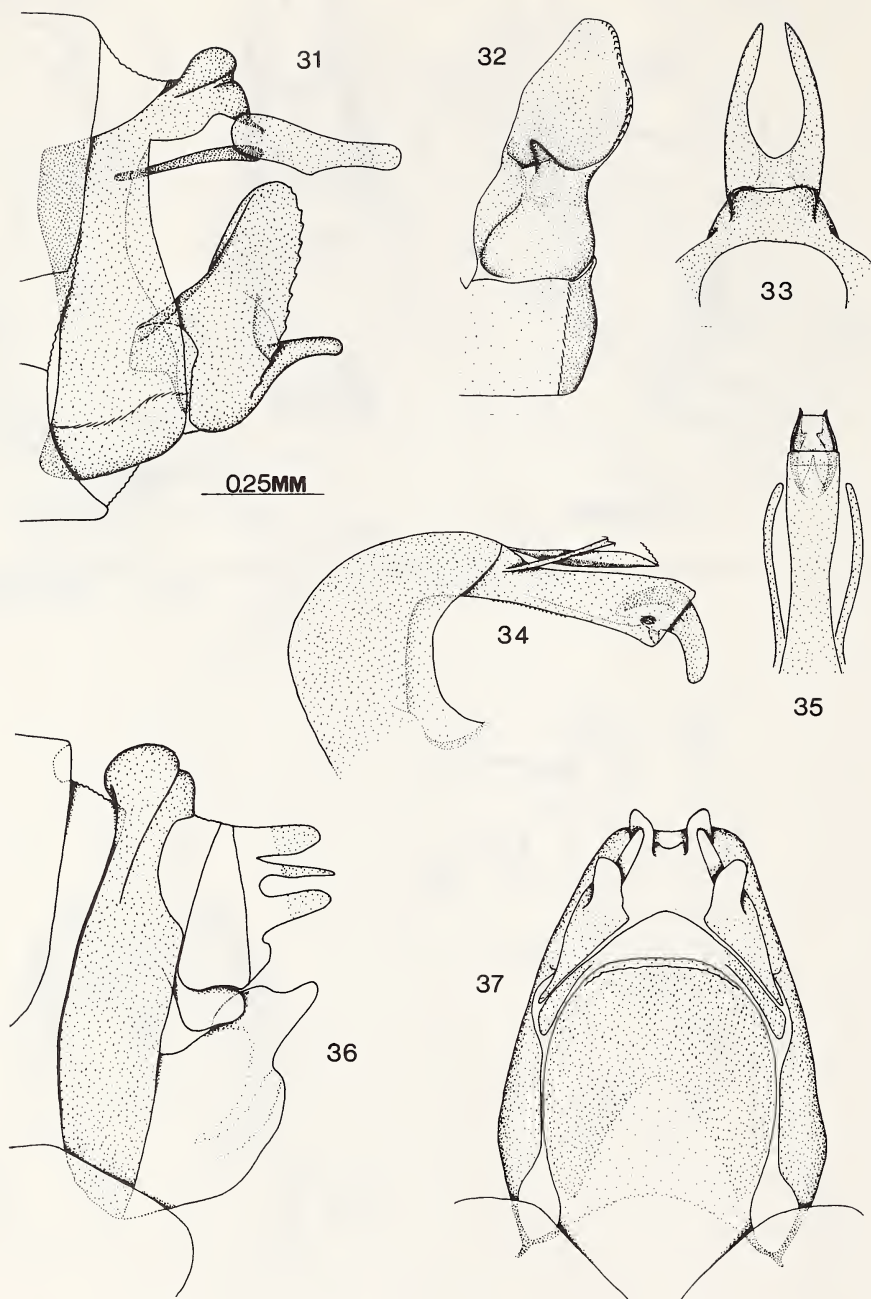
Fig. 31–37, *Parapsyche apicalis* (Banks): 31, genital capsule of male, lateral aspect; 32, right clasper of male, ventral aspect; 33, genital capsule of male, dorsal aspect; 34, aedeagus of male, lateral aspect; 35, aedeagus of male, distal half, ventral aspect; 36, genital segments of female, lateral aspect; 37, genital segments of female, ventral aspect.

0.5MM
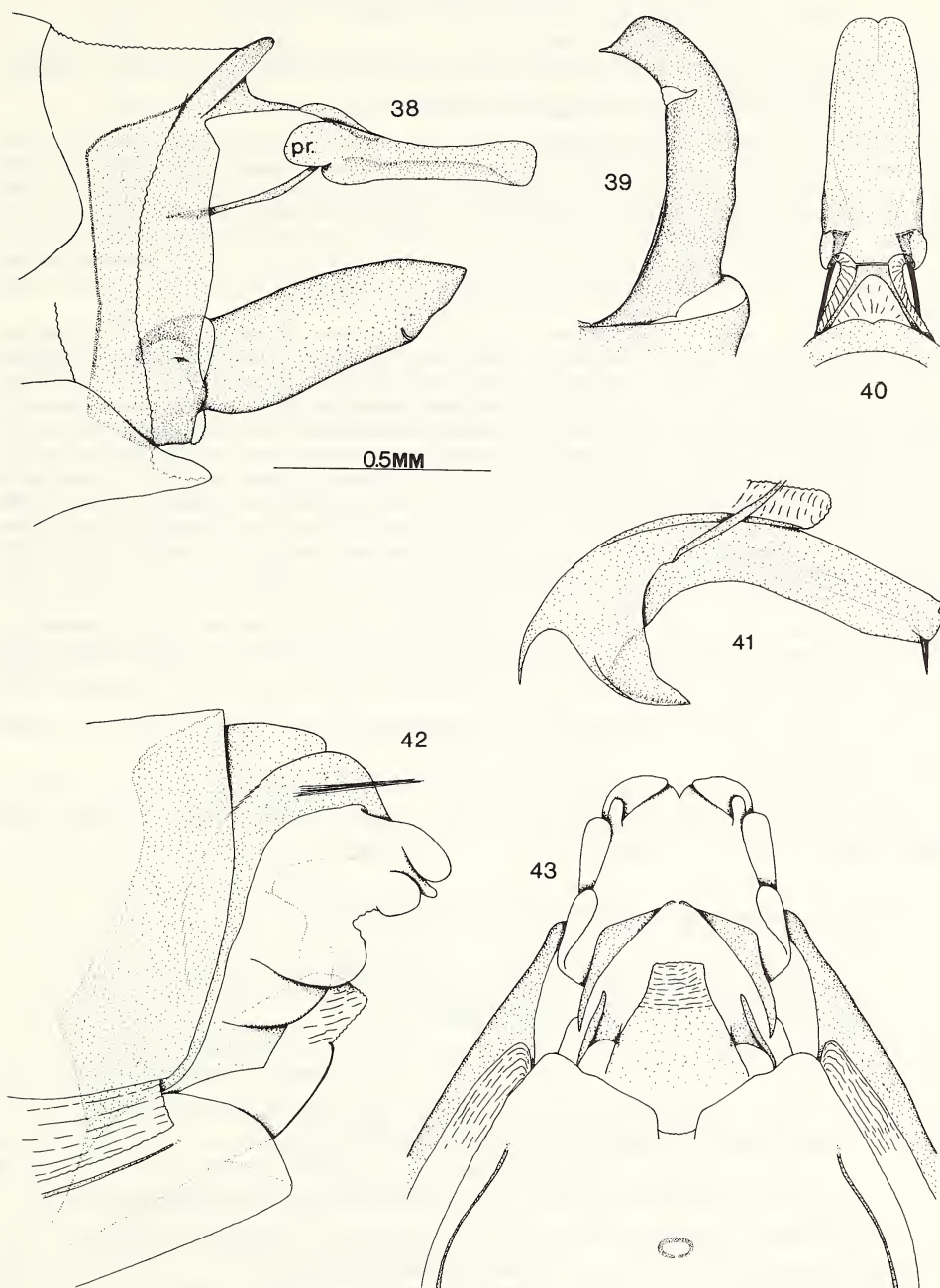
Fig. 38–43, *Parapsyche elsis* Milne: 38, genital capsule of male, lateral aspect; 39, right clasper of male, ventral aspect; 40, genital capsule of male, dorsal aspect; 41, aedeagus of male, lateral aspect; 42, genital segments of female, lateral aspect; 43, genital segments of female, ventral aspect. pr, preanal appendage.

THE FAMILY HYDROPSYCHIDAE CURTIS

Hydropsychidae Curtis, 1835:Pl. 544 (& text); Betten, 1934:116, 123, 176; Milne, 1936:63, 67; Ross, 1944:76; Wiggins, 1977:92; Schmid, 1980:55.
Hydropsychinae; (Subfamily of Phryganeidae) Burmeister, 1839:907.

Description.— Ocelli absent. Eyes very large in males of some species. Maxillary palpi with five articles in both sexes; basal article variable in length; fifth article very long, flagellate. Tibia and tarsus of female middle legs enlarged, flattened in many taxa. Spur formula generally 2,4,4. Sternite V in many taxa with lobe with aperture of internal gland. Fore- and hind-wings different in shape. Fore-wing smoothly, slightly broadened distally, with truncate apex (Fig. 3a). Hind-wing larger, more rounded (Fig. 3b). Venation complete, with five marginal forks (fI-fV) generally present in fore-wing, and fI-fIII and fV present in hind-wing. Discoidal and median cells closed in fore-wing; thyridial cell very long. In hind-wing Sc in contact with R1; discoidal and median cells open or closed; four free anal veins extended to wing margin.

Genitalia. Male. (Fig. 44–47, 469–472, 483–487). Quite similar in all genera. Segment IX in most taxa, short, well developed dorsally (Fig. 44, 469, 483). Segment X bulky, located roof-like over aedeagus, with various specifically characteristic lobes. Preanal appendages present; entirely integrated with segment X; reduced, simple tubercles, each with tuft of short hairs. Intermediate appendages absent. Claspers (inferior appendages) directed postero-dorsad; of two simple, slender articles; curved mesad (Fig. 45) and, as pair, pincer-like. Aedeagus large, with greatly expanded base (Fig. 46); entirely, or almost entirely, composed only of the phallotheca. Endotheca absent or minute; simple or complex.

Genitalia. Female. (Fig. 48–49, 473–474, 488–489). As in males, females are equaly similar in all genera. Sternite VIII more or less divided to two large lobes by postero-ventral fissure. Segment X large, roughly triangular in lateral aspect (Fig. 49); produced deeply ventrad. Dorsal extremity of segment X with two tufts of stout hairs (omitted from illustrations here). Segment XI basically high, oblique rectangle, clothed in short hairs; with two small, tube-like, papillate lobes with cerci between, latter in many taxa with vestiges of distal article. Vulval scale large, elongate, largely membranous, basally articulated with ventral extremity of segment X.

Hydropsychid larvae are filter-feeders, building a sheltered retreat with attached net projected into the current, which is typical. Macronematine larvae are more specialised in their structures, and frequent warmer, less turbulent waters. Very few species are recorded west of the Great Plains of North America, in the Cordillera. Larvae of some species live along wave-swept lake shores.

While retaining a basic uniformity throughout, the Hydropsychidae are represented by a multitude of species on every continent but Antarctica. In Canada are found six genera. The species known, or likely to be recorded from Canada number 72.

Key to known or potential genera of Hydropsychidae of Canada

1a		Discoidal and median cells of fore-wing small. Discoidal cell of hind-wing open. Fore-wing brown, barred with yellow . . . . Macronematinae Ulmer p. 173 . . . . *Macrostemum* Kolenati, p. 173
1b		Sternite V with long filament. Hind-wings large, rounded, with Sc and R1 markedly bowed distally (Fig. 4b). Antennae slightly crenate . . . . Diplectroninae Ulmer, p. 167 2
1c		Sternite V at most with lobe or faint prominence. Hind-wing constricted somewhat distally (Fig. 3b, 5b, 6b). Antennae slender, cylindrical . . . . Hydropsychinae Curtis, p. 23 3
2a	(1b)	Hind-wing apex rounded; with Sc and R1 bowed deeply apically (Fig. 4b) . . . . *Diplectrona modesta* Banks, p. 170
2b		Hind-wing apex more bluntly rounded (Fig. 1b); with Sc and R1 not bowed deeply apically . . . . *Aphropsyche doringa* Milne, p. 167
3a	(1c)	Stems of M and Cu1 of hind-wing parallel, very close together (Fig. 5b, 6b); fI present 4

3b   Stems of hind-wing M and Cu1 not parallel, not close; fI absent (Fig.
         3b) . . . . *Cheumatopsyche* Wallengren, p. 23
4a (3a) In fore-wing, cross-veins M3+4-Cu1 and Cu1-Cu2 close (Fig. 6a); A in
         contact with Cu2 prior to wing margin. Hind-wing median cell open (Fig.
         6b) . . . . *Potamyia flava* (Hagen), p. 164
4b   In fore-wing, cross-veins M3+4-Cu1 and Cu1-Cu2 clearly separated (Fig.
         5a); A terminated at wing margin. Hind-wing median cell closed (Fig.
         5b) . . . . *Hydropsyche* Pictet, p. 76

The Subfamily Hydropsychinae Curtis

Hydropsychinae Curtis, 1835: pl. 544 (text); Betten, 1934:118, 177; Milne, 1936:67; Ross & Unzicker,
     1977:298; Wiggins, 1977:93; Schmid, 1979:48; Schmid, 1980:48.

Description.— Antennae slender, slightly longer than fore-wings, especially in male. Maxillary palpi with first and second articles equal; third and fourth articles short. Vertex with more than two warts. Tibia and tarsus of female middle legs flattened, enlarged. Fore-wing slightly, evenly widened distad (Fig. 3a, 5a, 6a); distally truncate. Hind-wing (Fig. 3b, 5b, 6b) slightly larger than fore-wing; with evenly rounded anal edge, but distally constricted. Venation complete; fI-fV present in fore-wing, fI-fIII and fV in hind-wing. Discoidal and median cells rather small; fI and fIII petiolate. Hind-wing discoidal cell closed; median cell open (Fig. 6b) or closed (Fig. 5b).

Genitalia. Male. (Fig. 44–47, 182–186, 463–466). Segment IX rather short; with postero-lateral edge more or less projected posterad. Segment X either simple, or bilobed with distal lobes or processes. Claspers (inferior appendages) slender, of two articles. Aedeagus simple or with complex apex.

Genitalia. Female. (Fig. 48–49, 187–188, 467–468). Segment X with only narrow ventro-lateral extremity which serves to support vulval scale. Dorso-lateral face of segment X with more or less evident clasper receptacle, or apparently absent.

Genus *Cheumatopsyche* Wallengren
Maps 7–30; Fig. 3, 44–181

Cheumatopsyche Wallengren, 1891:138, 142; Denning, 1943:138; Ross, 1944:108; Gordon, 1974:117; Wiggins, 1977:100;
     Schmid, 1980:60.
Ulmeria Navás, 1918:15; Navás, 1933:98.
Hydropsychodes Ulmer, 1905:34; Kimmins, 1963:130.

Description.— Small, slender insects. Tarsal claws variously deformed or normal. Cross-veins M3+4-Cu1 and Cu1-Cu2 of fore-wings adjacent (Fig. 3a). Hind-wing fI absent; median cell open; stems of M and Cu1 divergent, not very close (Fig. 3b).

Genitalia. Male. (Fig. 44–47, *etc.*). Very similar to *Hydropsyche* species. Segment IX postero-lateral angle generally less prominent, more ventrad (Fig. 44, 50). Segment X less bulky; terminated in two or four setose, specifically distinct lateral lobes (Fig. 47, 53), separated by inconspicuous median bridge. Claspers (inferior appendages) slender, with distal article of many species curved mesad, claw-like (Fig. 45). Aedeagus proximally very large; simple; distally terminated by two large endothecal valves.

Genitalia. Female. (Fig. 48–49, *etc.*). Tergite VIII with posterior edge not notched. Sternite VIII divided longitudinally to two halves or lobes. Segment X without postero-lateral margin produced posterad. Clasper receptacle or not; the term "chimney" is used here to refer to the 'apical two-thirds' of clasper receptacle (Jordan, 1974).

Wiggins (1977), partly quoting from earlier authors, wrote us that *Cheumatopsyche* larvae tend to be more dominant in warmer streams than *Hydropsyche* larvae, and to be more pollution tolerant than most other species of caddisflies. Larvae of this genus have also been found as deep as 20 cm in stream-bed gravels. Gut-content analysis indicates that feeding is largely on algae and small animals, with little detrital component.

Cheumatopsyche is represented in all regions but the Neotropical and the Antarctic continent. Gordon (1974) identifies 39 species known from the Nearctic region. In this work I deal with 24 species known from Canada, or potentially to be found here.

Key to known or potential species of *Cheumatopsyche* of Canada (Adapted from Gordon, 1974)

1a   Males 2

1b   Females 25

2a   (1a)   Distal article of clasper not produced to tapered apex in lateral aspect (Fig. 50); short, blunt . . . . *sordida* complex, p. 27 3

2b   Distal article of clasper long, tapered (Fig. 135) . . . *gracilis* complex, p. 32 4

3a   (2a)   Aedeagus base very large (Fig. 46). Lobes of tergum X, acuminate hooks directed dorsad (Fig. 44). Tergum X with long, sclerotised, distally bulbous, median process emergent posteriorly from below tergum (Fig. 44, 47) . . . . *C. minuscula* (Banks), p. 27

3b   Aedeagus base moderately large at most (Fig. 52). Lobes of tergum X wide in lateral aspect (Fig. 50). Median process absent . . . .
. . . . *C. sordida* (Hagen), p. 28

4a   (2b)   Dorsum of tergite X domed (Fig. 99) . . . . *C. wabasha* Denning, p. 46

4b   Dorsum of tergite X flat (Fig. 142) 5

5a   (4b)   Dorsal lobes of segment IX indistinctly defined, with single seta (Fig. 130). Aedeagus elongate, almost linear . . . . *C. vannotei* Gordon, p. 60

5b   Dorsal lobes of segment IX clearly defined, with numerous setae (Fig. 163). Aedeagus not elongate, not linear 6

6a   (5b)   Preanal appendages vertically long, linear in lateral aspect (Fig. 163) . . . .
. . . . *C. mollala* Ross, p. 65

6b   Preanal appendages vertically short, circular in lateral aspect (Fig. 63) 7

7a   (6b)   Distal lobes of tergum X with apices elongate, reflexed (Fig. 59, 66, 72) 8

7b   Distal lobes of tergum X with apices not reflexed (Fig. 148) 10

8a   (7a)   Distal article of clasper, in posterior aspect, short (Fig. 64); not fully curved; distal portion straight or possibly slightly recurved. Lobes of tergum X broad, rounded in lateral aspect (Fig. 63); anterad of turned-up distal edges of tergum; lobes not visible in posterior aspect . . . .
. . . . *C. pinaca* Ross, p. 32

8b   Distal article of clasper, in posterior aspect (Fig. 57, 70), longer; entire article almost straight. Distal lobes of tergum X with apices visible in posterior aspect (Fig. 59, 72); distal edge of tergum turned dorsad (Fig. 59), or not (Fig. 72) 9

9a   (8b)   Distal article of clasper, in lateral aspect (Fig. 56) hooked sharply dorsad at tip. Distal edge of tergum X produced posterad of distal lobes, flared dorsad . . . . *C. speciosa* (Banks), p. 32

9b   Distal article with only slightly curved tip (Fig. 69). Distal edge of tergum X not produced posterad of distal lobes, not flared dorsad . . . .
. . . . *C. lasia* Ross, p. 32

10a   (7b)   Distal article of clasper two-thirds length of basal article (Fig. 145, 146) . .
. . . . *C. oxa* Ross, p. 64

10b   Distal article, at most, only half length of basal article (Fig. 107, 113, 129) 11

11a (10b) Distal lobes of tergum X circular or ovate dorsally, in posterior aspect (Fig. 110, 116, 131) 12

11b   Distal lobes of tergum X not circular or ovate dorsally, in posterior aspect

. . . . *C. campyla* Ross, p. 38

24b   Dorso-lateral lobes of segment IX barely evident (Fig. 103) . . . .
. . . . *C. logani* Gordon, p. 48

25a (1b) Clasper receptacle absent, or not visible, or minute in lateral aspect (Fig.
          49, 55) . . . . *sordida* complex, p. 27 26

25b   Clasper receptacle clearly visible in lateral aspect (Fig. 60, 68, 156) . . . . .
. . . . *gracilis* complex, p. 32 27

26a (25a) Clasper receptacle, in lateral aspect (Fig. 49), a minute circle high up on
          segment X . . . . *C. minuscula* (Banks), p. 27

26b   Clasper receptacle, in lateral aspect (Fig. 55), very small, triangular
          invagination high up on segment X on border between darker anterior bulk
          of segment, and paler posterior area . . . . *C. sordida* (Hagen), p. 28

27a (25b) Clasper receptacle short, small, located high on segment X (Fig. 86, 174, 181) . . 28

27b   Clasper receptacle longer, larger, in most specimens located at a level
          ventrad of ventral lobe of segment XI (Fig. 97, 112, 118, *etc.*) 30

28a (27a) Inner end of clasper receptacle, in lateral aspect, apparently not open,
          rounded (Fig. 174, 181) 29

28b   Inner end of clasper receptacle, in lateral aspect, clearly open (Fig. 86) . . .
. . . . *C. mickeli* Denning, p. . . .

29a (28a) Inner end of clasper receptacle, in lateral aspect, directed anterad (Fig.
          181). Vulval scale without sclerotised band . . . . *C. enonis* Ross, p. 66

29b   Inner end of clasper receptacle, in lateral aspect, directed dorsad (Fig.
          174). Vulval scale with very narrow sclerotised strap, proximal end
          abruptly flared . . . . *C. burksi* Ross, p. 65

30a (27b) Clasper receptacle outer edge without of marginal incision (Fig. 60, 68,
          118, 140, 156, 162, 168) 31

30b   Clasper receptacle outer edge with incision, either rounded or angular (Fig.
          74, 80, 92, 97, 112, 124, 134, 150) 37

31a (30a) Posterior margin of segment X overlapped by marginal flange developed
          from outer edge of clasper receptacle 32

31b   No such flange or overlap (Fig. 60, 68, 118, 140, 168) 33

32a (31a) Development of flange dorsad, along posterior edge of segment X; clasper
          receptacle apparently with two chimneys (Fig. 156) . . . .
. . . . *C. aphanta* Ross, p. 64

32b   No such development of flange (Fig. 162) . . . . . . *C. halima* Denning, p. 65

33a (31b) Anterior end of outer margin of clasper receptacle continued on lateral face
          of segment X as thin, black line; length various with species (Fig. 60, 118, 140) . . 34

33b   No such continuation of outer margin (Fig. 68, 168) 36

34a (33a) Clasper receptacle tubular (Fig. 60) . . . . *C. speciosa* (Banks), p. 32

34b   Clasper receptacle papillate (Fig. 118, 140) 35

35a (34b) Clasper receptacle long, located dorsally (Fig. 140) . . . .
. . . . *C. gracilis* (Banks), p. 60

35b   Clasper receptacle small, located at level ventrad of ventral lobe of segment
          XI (Fig. 118) . . . . *C. pettiti* (Banks), p. 48

36a (33b) Posterior edge of each half of sternite VIII with small, rounded process
          close to lateral corner (Fig. 68) . . . . *C. pinaca* Ross, p. 32

36b No such process present .... *C. mollala* Ross, p. 65

37a (30b) Incision of outer margin of clasper receptacle angled (Fig. 80, 92, 97, 134) 38

37b Incision of outer margin of clasper receptacle rounded; large (Fig. 112, 150), through small (Fig. 74), to minute (Fig. 124) 41

38a (37a) Inner opening of clasper receptacle, in lateral aspect, visible (Fig. 80, 92) 39

38b Inner opening of clasper receptacle not visible in lateral aspect, rounded (Fig. 97, 134) 40

39a (38a) Incision of clasper receptacle margin directed anterad (Fig. 80) ....
.... *C. pasella* Ross, p. 38

39b Incision of clasper receptacle margin directed dorsad (Fig. 92) ....
.... *C. campyla* Ross, p. 38

40a (38b) Anterior end of clasper receptacle margin extended antero-ventrad across lateral face of segment X as fine, sinuate, dark line (Fig. 134) ....
.... *C. h. harwoodi* Denning, p. 54

40b No such continuation of clasper receptacle margin (Fig. 97) ....
.... *C. ela* Denning, p. 39

41a (37b) Inner opening of clasper receptacle visible in lateral aspect (Fig. 74, 150) 42

41b Inner opening of clasper receptacle not visible in lateral aspect (Fig. 112, 124) .. 43

42a (41a) Inner opening of clasper receptacle as wide as chimney (Fig. 150) ....
.... *C. oxa* Ross, p. 64

42b Inner opening narrower than chimney (Fig. 74) ...... *C. lasia* Ross, p. 32

43a (41b) Marginal incision of clasper receptacle margin narrow, minute; anterior end of margin associated with fine, dark, sinuate line just anterad (Fig. 124) .... *C. helma* Ross, p. 54

43b Marginal incision of clasper receptacle wide, of medium size; no fine, dark line associated with anterior end of margin (Fig. 112) ....
.... *C. smithi* Gordon, p. 48

Gordon (1974) divides this genus into *sordida* and *gracilis* complexes, which are included in the above key. These complexes are each further subdivided to species groups. Other than presenting the species included here in the order of complexes, species groups, and species used by Gordon, no further details are given regarding them. It is considered that the minutiae involved are beyond the scope of the present work.

<div align="center">

THE *SORDIDA* COMPLEX

THE *SORDIDA* GROUP

Cheumatopsyche minuscula (Banks)

Map 7; Fig. 44–49

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Hydropsyche minuscula Banks, 1907:130; Milne, 1936:73 (as synonym of *C. sordida*).
Hydropsychodes minuscula; Carpenter, 1933:43; Betten, 1934:195.
Cheumatopsyche minuscula; Ross, 1938c:15; Denning, 1943:142; Ross, 1944:110; Gordon, 1974:127.
Cheumatopsyche montrealensis Nimmo, 1966a:689; Gordon, 1974:127.

Description.— Male fore-wing length 7.72 mm; red-brown, without evident pattern. Hind-wing paler than fore-wing, but distinctly tinted. Antennae greyish brown; each flagellar annulus with oblique, faint, darker band around mid-point. Vertex dark red-brown; warts slightly paler, surrounded by very dark boundary. Spurs dark brown; lateral member of middle and hind-leg pairs slightly smaller than mesal companions. Thorax deep red-brown dorsally, to paler

laterally. Legs straw-coloured, with tarsal articles darker.

Genitalia. Male. (Fig. 44–47). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec – Holotype of *C. montrealensis* Nimmo). Males distinguished by distal lobes of tergum X small, hooked dorsad in lateral aspect (Fig. 44); by blunt, rounded distal article of clasper in lateral aspect (Fig. 44); and by long, thin, distally bulbous process emergent from beneath tergum X (Fig. 44, 47).

Genitalia. Female. (Fig. 48–49). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Females distinguished by minute, circular or elliptical clasper receptacle high on lateral face of segment X, in lateral aspect (Fig. 49).

Biology.— Available records indicate that larvae of this species prefer fair-sized to extremely large, turbulent, rubble-bottomed rivers. Flight dates range from June 6 to September 9, peaking in late June and July.

Distribution.— To date the species has been recorded from Manitoba and the lower St Lawrence River in the north, to Oklahoma and Georgia in the south (Map 7). In Canada it is now known from eastern Manitoba to the Saguenay River of Québec, but most records are from southern Québec and Ontario.

Cheumatopsyche sordida (Hagen)
Map 8; Fig. 50–55

Hydropsyche sordida Hagen, 1861:290; Milne, 1936:70, 72, 73.
Hydropsychodes sordida; Ulmer, 1905b:100; Betten, 1934:196.
Cheumatopsyche sordida; Ross, 1938c:15; Denning, 1943:142; Ross, 1944:110; Gordon, 1974:126.

Description.— Male fore-wing length 6.86 mm; uniform rich dark brown. Hind-wing uniformly, palely tinted deep brown. Antennae deep brown; basal five flagellar annuli with oblique, darker bands. Female with six banded annuli. Vertex very dark brown. Spurs brown; lateral member of middle and hind-leg pairs notably shorter than mesal companions, in males; not so in females. Thorax very dark brown, to red-brown laterally. Legs yellow-brown.

Genitalia. Male. (Fig. 50–53). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Males distinguished by short, blunt distal article of clasper, in lateral aspect (Fig. 50); by widely separated distal lobes of tergum X in posterior aspect (Fig. 53), with dorso-lateral angles toothed; and by distal portion of aedeagus phalotheca deeply keeled ventrally (Fig. 52).

Genitalia. Female. (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Females differentiated by very small, triangular clasper receptacle, in lateral aspect (Fig. 55), located well dorsad on lateral face of segment X and with outer margin as part of boundaryline between anterior darker part of segment, and posterior lighter part.

Biology.— Available records indicate that larvae of this species inhabit a wide variety of flowing waters in Canada, ranging from small to very large rivers, and from slow-flowing boreal waters to fast, turbulent rivers. Flight dates range from June 7 to August 14, with possible peak about end of June, early July.

Distribution.— Recorded from Manitoba to New Brunswick in the north, to Texas and Georgia in the south (Map 8). In Canada it is recorded from Lake Winnipeg to southern New Brunswick, with most records being from the Ottawa River drainage.
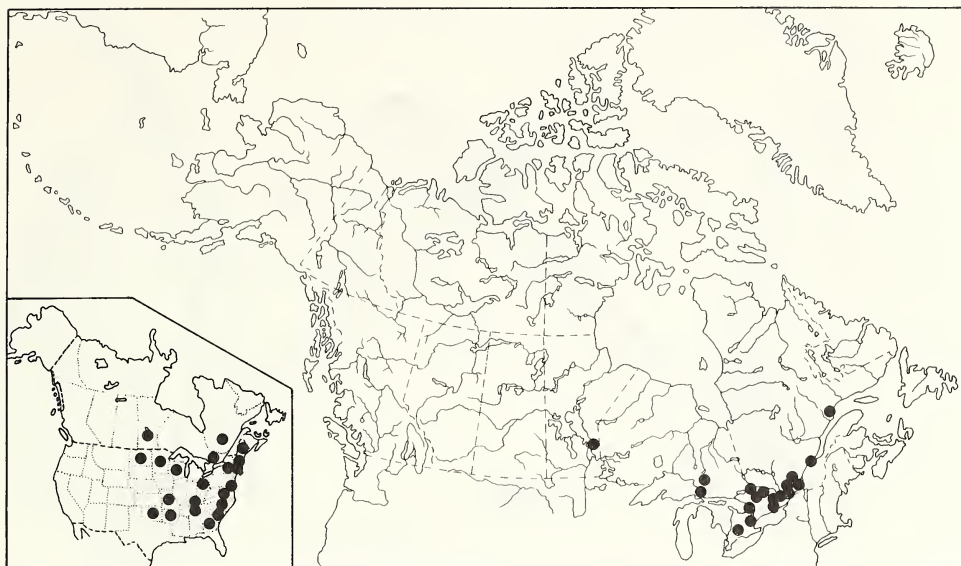
Map 7. Collection localities for *Cheumatopsyche minuscula* (Banks) in Canada, with known distribution in North America by state or province.
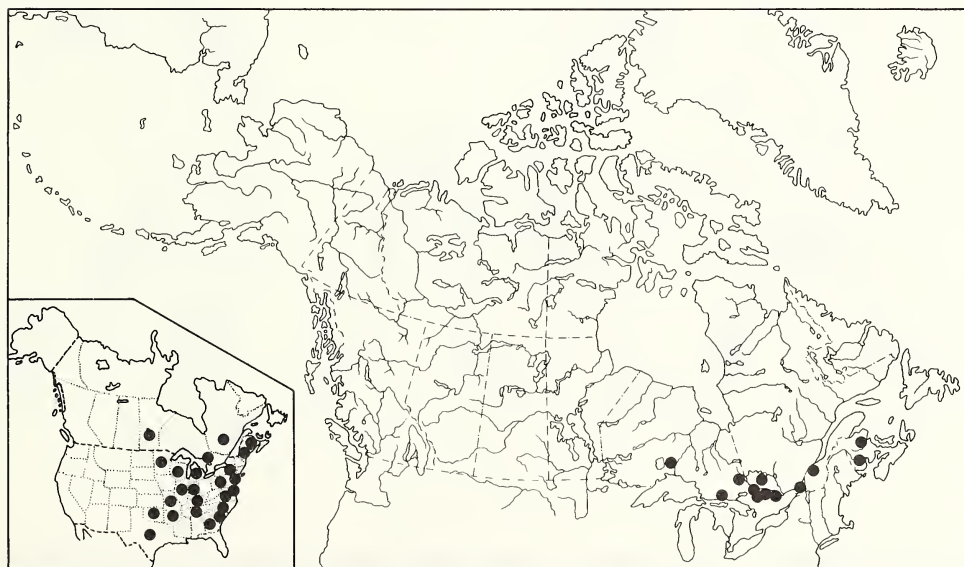
Map 8. Collection localities for *Cheumatopsyche sordida* (Hagen) in Canada, with known distribution in North America by state or province.
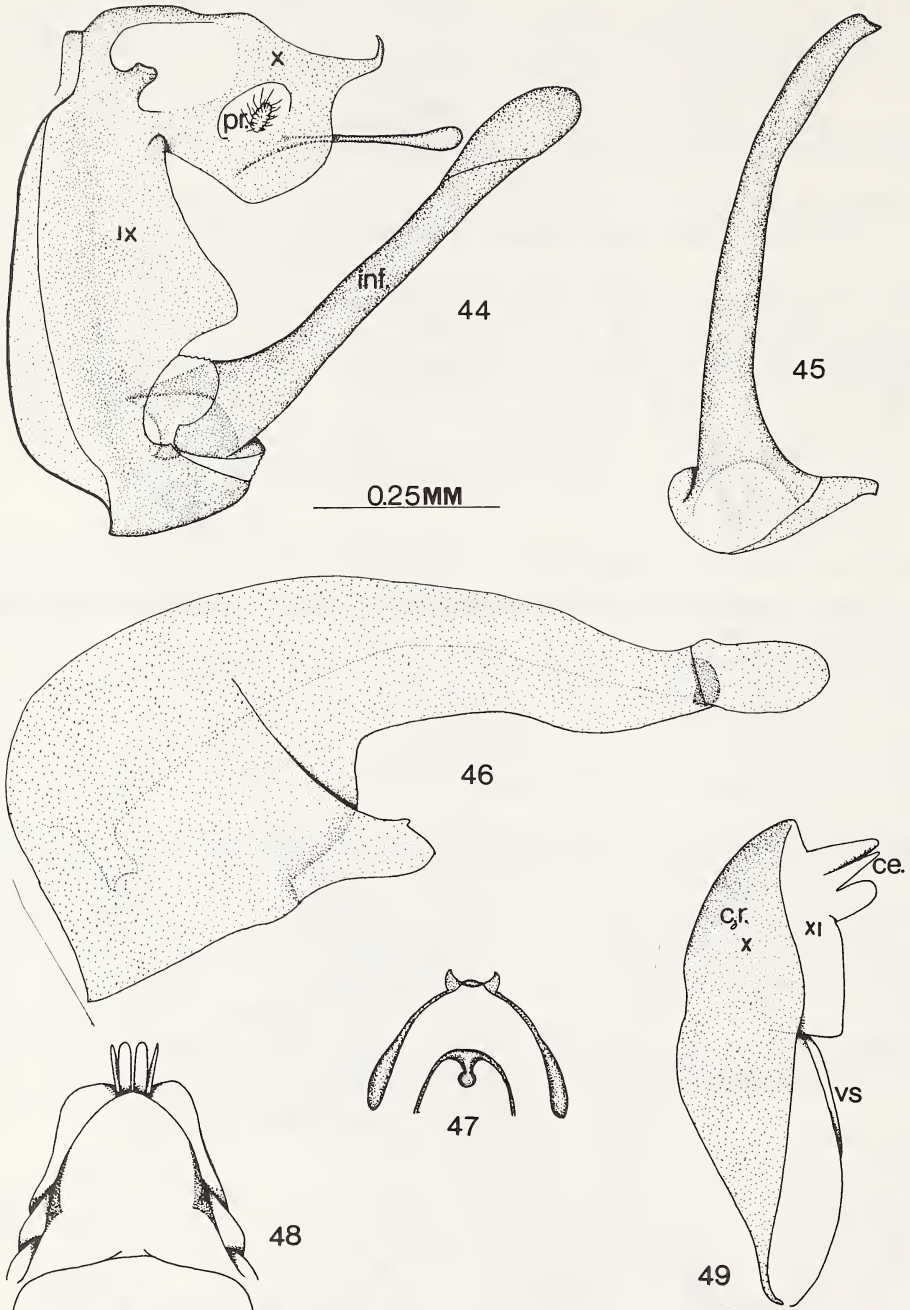
Fig. 44–49, *Cheumatopsyche minuscula* (Banks): 44, genital capsule of male, lateral aspect; 45, left clasper of male, posterior aspect; 46, aedeagus of male, lateral aspect; 47, segment X of male, posterior aspect; 48, genital segments of female, dorsal aspect; 49, genital segments of female, lateral aspect. inf, inferior appendage (clasper); pr, preanal appendage; cr, clasper receptacle; vs, vulval scale.
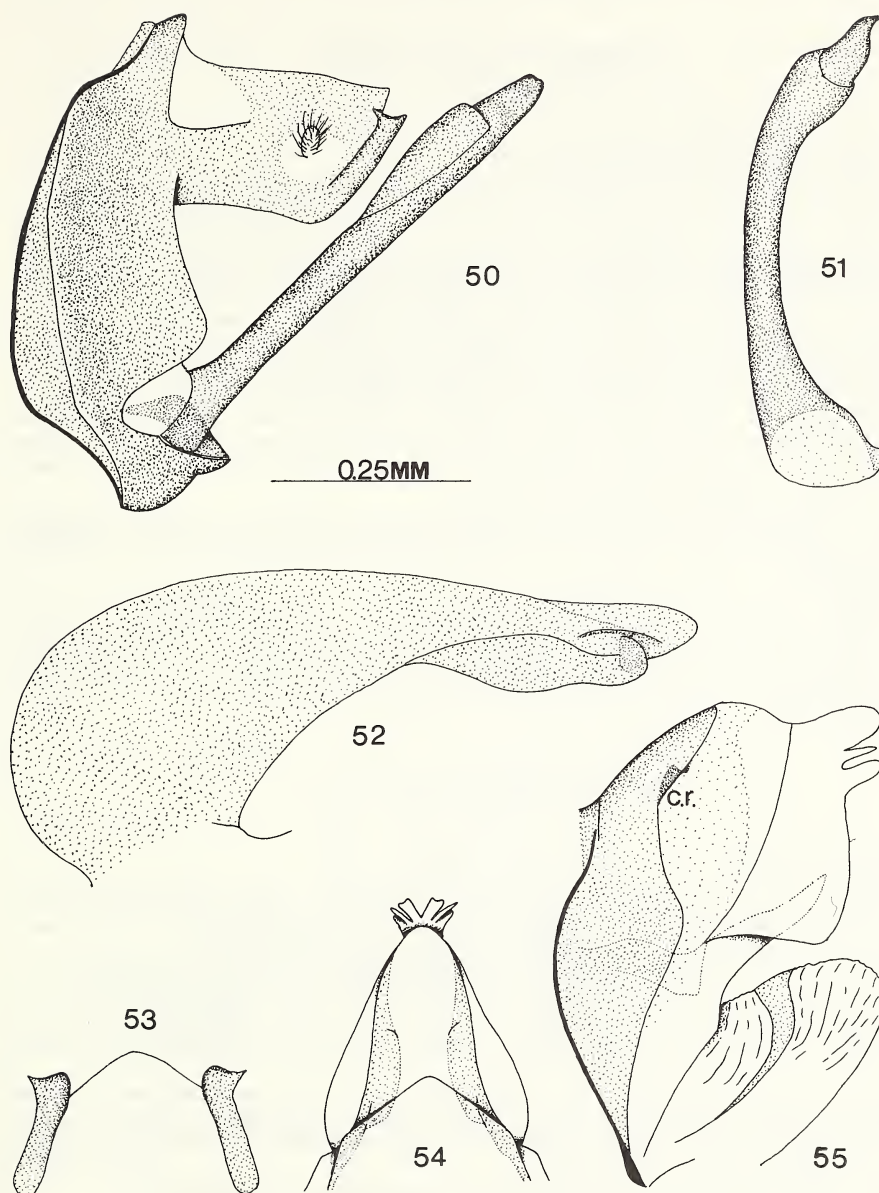
Fig. 50–55, *Cheumatopsyche sordida* (Hagen): 50, genital capsule of male, lateral aspect; 51, left clasper of male, posterior aspect; 52, aedeagus of male, lateral aspect; 53, segment X of male, posterior aspect; 54, genital segments of female, dorsal aspect; 55, genital segments of female, lateral aspect. cr, clasper receptacle.

THE *GRACILIS* COMPLEX
THE *SPECIOSA* GROUP

Cheumatopsyche speciosa (Banks)
Map 9; Fig. 56–62

Hydropsyche speciosa Banks, 1904a:214; Milne, 1936:71, 73.
Hydropsychodes speciosa; Neave, 1929:190; Betten, 1934:197.
Cheumatopsyche speciosa; Ross, 1938c;15; Denning, 1943:154; Ross, 1944:114; Gordon, 1974:134.

Description.— Male fore-wing length 5.54 mm; grey-brown with scattered irroration and larger areas of hyaline membrane which give transverse banded appearance. Antennae yellowish brown; basal five flagellar annuli each with slightly darker, oblique band (not evident in female). Vertex reddish brown. Spurs yellow; members of each pair essentially equal. Thorax deep reddish brown, to yellowish brown laterally. Legs straw-coloured.

Genitalia. Male. (Fig. 56–59). (Specimen from Whitemud Ck, Ellerslie, Alberta). Males distinguished by deep cleft between dorsum of segment IX and tergum X, in lateral aspect (Fig. 56); by distal lobes of segment X adjacent to this cleft, and posterior extremity of tergum X flared dorso-laterad as pair of flanges (Fig. 56, 59); and by long, slender distal article of clasper, more or less linear in posterior aspect (Fig. 57), sinuate, hooked dorsad in lateral aspect (Fig. 56).

Genitalia. Female. (Fig. 60–62). (Specimen from Whitemud Ck, Ellerslie, Alberta). Females distinguished by postero-lateral angle of each half of sternite VIII (Fig. 62) with small, triangular process; by inner opening of clasper receptacle not visible in lateral aspect (Fig. 60), receptacle of more or less uniform width; and by outer margin of clasper receptacle with anterior extremity higher than posterior extremity.

Biology.— This species is recorded from small, sluggish streams, and the largest, turbulent, rubble-bottomed rivers. Flight dates range from July 6 to August 29, with a diffuse peak in late June and July.

Distribution.— Recorded from Alberta to Labrador in the north, to Oklahoma and South Carolina in the south (Map 9). Canadian records are thinly scattered from east of the Rocky Mountain Foothills in Alberta, to northern Québec and Labrador in the east, and south to the United States border.

Cheumatopsyche pinaca Ross
Map 10; Fig. 63–68

Cheumatopsyche pinaca Ross, 1941:82; Ross, 1944:294; Gordon, 1974:133.

Description.— Male fore-wing length 5.75 mm; pale brown; faintly irrorate. Antennae orange-brown; basal five flagellar annuli each with oblique, darker band. Vertex dark brown; warts paler. Spurs brownish yellow; lateral member of middle leg pairs notably shorter than mesal companions. Thorax orange-brown. Legs straw-coloured.

Genitalia. Male. (Fig. 63–66). (Specimen from southern Appalachians, USA). Males distinguished by distal lobes of tergum X, in lateral aspect, short, rounded (Fig. 63); by extreme distal edge of tergum X flared dorso-laterad as pair of triangular flanges [distal lobes not visible in posterior aspect (Fig. 66)]; by distal article of clasper short, sharply but smoothly tapered distad, hooked dorsad in lateral aspect (Fig. 63); and by distal end of aedeagus slightly keeled ventrally (Fig. 65).

Genitalia. Female. (Fig. 67–68). (Specimen from southern Appalachians, USA). Females differentiated by lateral corner of each half of sternite VIII with short, rounded process (Fig. 68); by sclerotised band of vulval scale very wide, saddle-like across dorsum of scale; by clasper receptacle, in lateral aspect, papillate; and by anterior end of clasper receptacle outer margin much higher than posterior end.

Biology.— Neves (1979) records flight period in Massachusetts as June to August.

Distribution.— This species, not yet recorded from Canada, is recorded from Maine to Florida in the United States, west to Tennessee (Map 10).

Cheumatopsyche lasia Ross
Map 11; Fig. 69–74

*Cheumatopsyche lasia* Ross, 1938b:154; Denning, 1943:153; Ross, 1944:114; Gordon, 1974:132.

Description.— Male fore-wing length 4.3 mm; uniform golden brown. Hind-wing palely tinted golden brown. Antennae yellow-brown; with at least basal six flagellar annuli each with oblique, darker band. Vertex deep red-brown; warts rather paler. Spurs yellow; lateral member of mid-leg pairs notably shorter than mesal companions. Thorax very deep red-brown, to paler grey-brown laterally. Legs yellow-brown.

Genitalia. Male. (Fig. 69–72). (Specimen from Red Deer R., Drumheller, Alberta). Males distinguished by segment IX with distinct dorsal lobes (Fig. 69); by distal lobes of Tergum X projected well dorsad of main body of tergum X, in lateral aspect; and by these distal lobes with distinct basal processes, best seen in posterior aspect (Fig. 72).

Genitalia. Female. (Fig. 73–74). (Specimen from Brazos R., Palo Alto Co., Texas, USA). Females distinguished by clasper receptacle slightly expanded distally (Fig. 74); by inner opening visible in lateral aspect, narrower than chimney of receptacle, directed postero-dorsad; by outer margin of receptacle incised, incision small, rounded, directed antero-dorsad; by anterior end of receptacle outer margin higher at anterior end than posterior end; and by sclerotised strap of vulval scale broad, saddle-like across dorsal area of scale.

Biology.— Ross (1944) records the Illinois flight period as May to August, peaking in July and August. Available records from western Canada are for mid-July. It appears that adults emerge from the slower, less turbulent creeks and large rivers.

Distribution.— Recorded from México north to Alberta and Saskatchewan in Canada, and east to Illinois (Map 11). In western Canada it is recorded only from the South Saskatchewan River drainage.
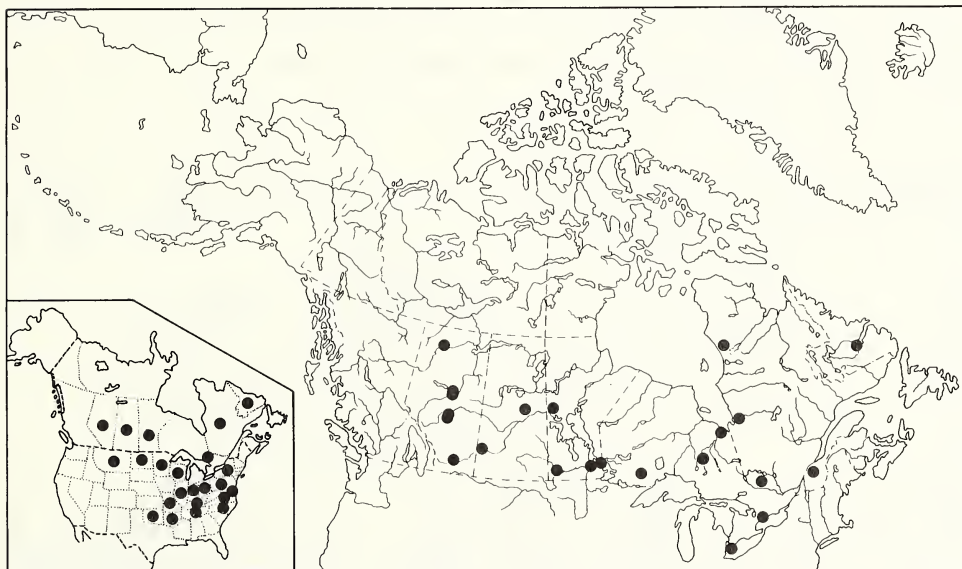
Map 9. Collection localities for *Cheumatopsyche speciosa* (Banks) in Canada, with known distribution in North America by state or province.
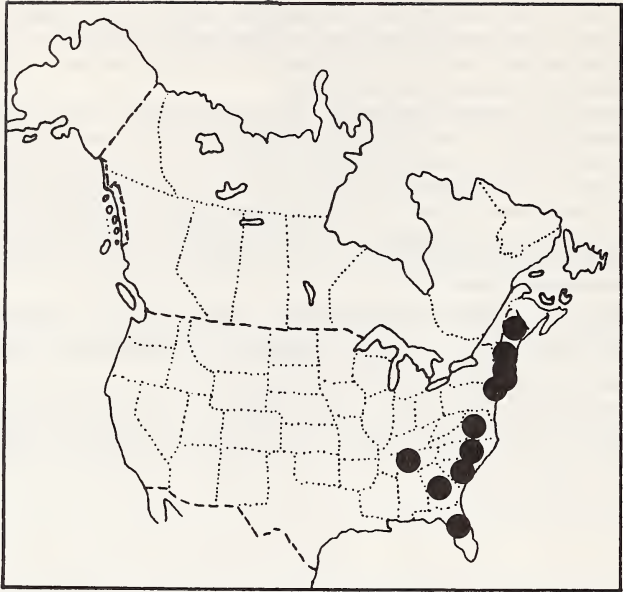
Map 10. Known distribution of *Cheumatopsyche pinaca* Ross in North America, by state.

Map 11. Collection localities for *Cheumatopsyche lasia* Ross in Canada, with known distribution in North America by state or province.
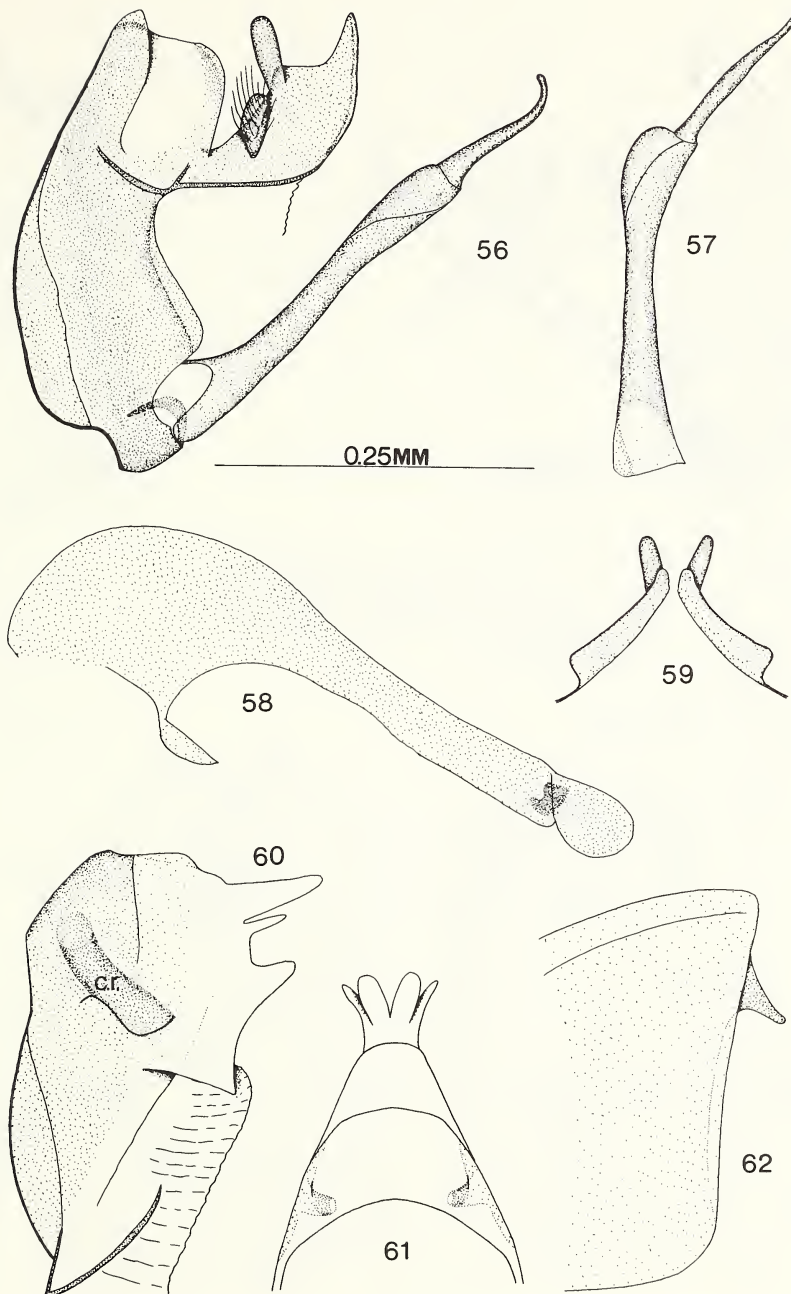
Fig. 56–62, *Cheumatopsyche speciosa* (Banks): 56, genital capsule of male, lateral aspect; 57, left clasper of male, posterior aspect; 58, aedeagus of male, lateral aspect; 59, segment X of male, posterior aspect; 60, genital segments of female, lateral aspect; 61, genital segments of female, dorsal aspect; 62, left half of sternite VIII of female, lateral aspect. cr, clasper receptacle.
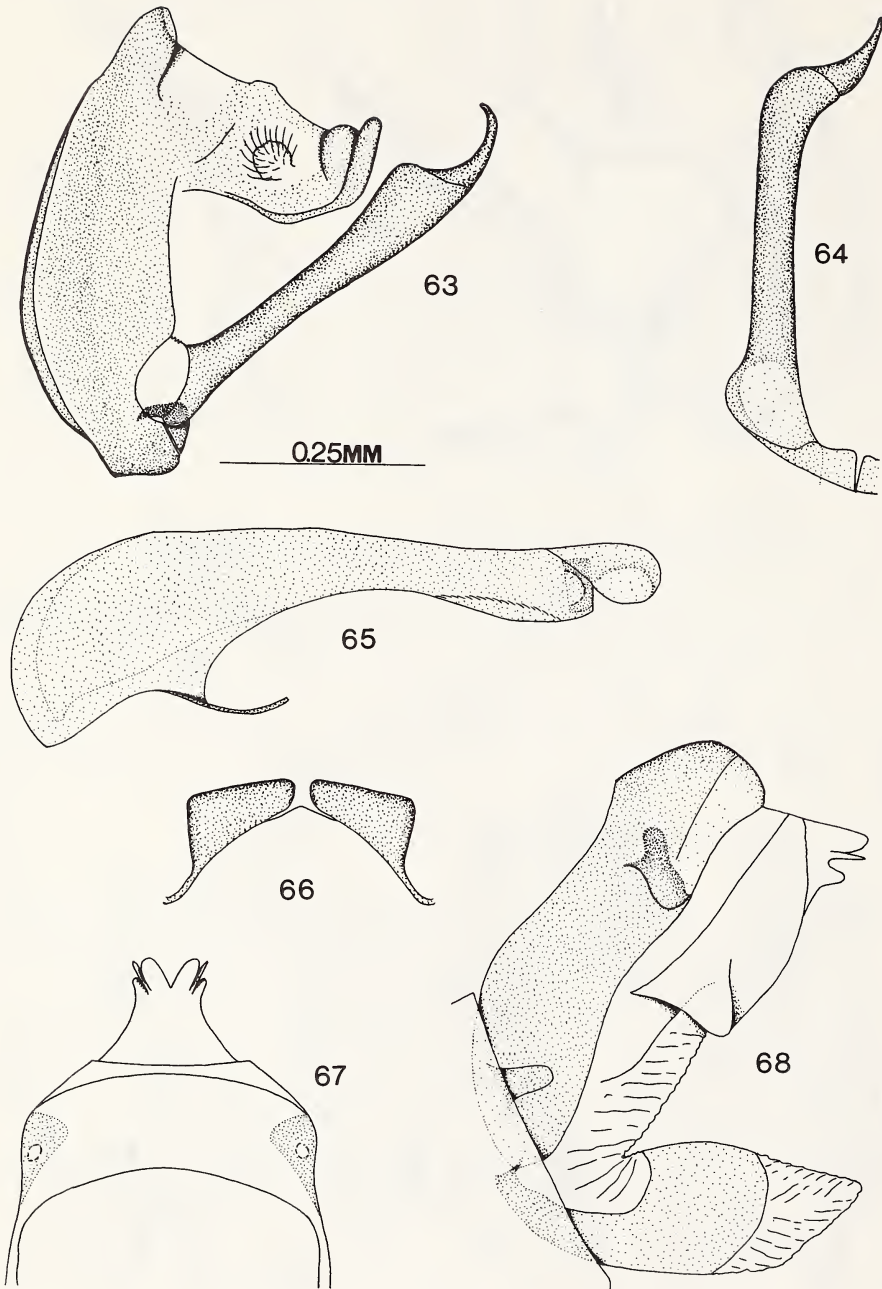
Fig. 63–68, *Cheumatopsyche pinaca* Ross: 63, genital capsule of male, lateral aspect; 64, left clasper of male, posterior aspect; 65, aedeagus of male, lateral aspect; 66, segment X of male, posterior aspect; 67, genital segments of female, dorsal aspect; 68, genital segments of female, lateral aspect.
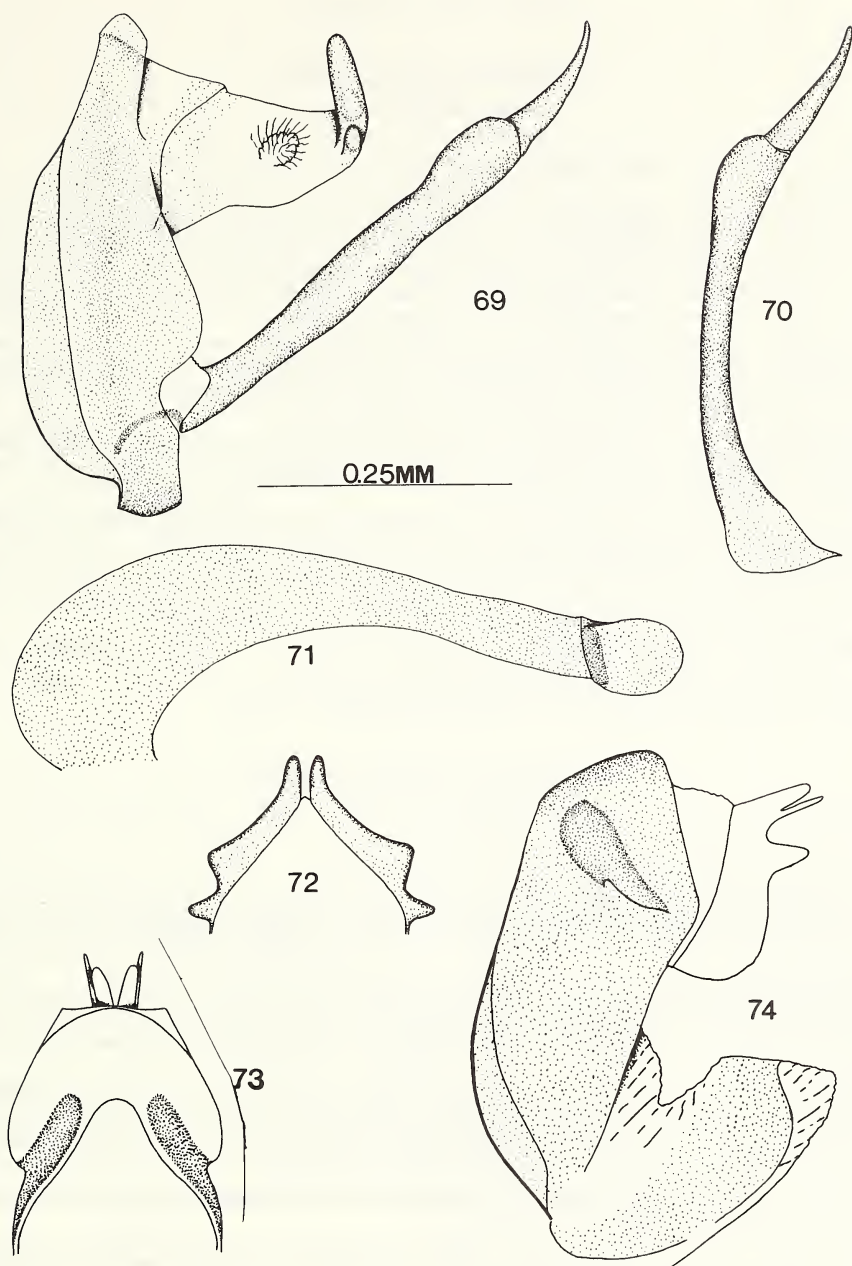
Fig. 69–74, *Cheumatopsyche lasia* Ross: 69, genital capsule of male, lateral aspect; 70, left clasper of male, posterior aspect; 71, aedeagus of male, lateral aspect; 72, segment X of male, posterior aspect; 73, genital segments of female, dorsal aspect; 74, genital segments of female, lateral aspect.

THE *CAMPYLA* GROUP

Cheumatopsyche pasella Ross
Map 12; Fig. 75–80

Cheumatopsyche pasella Ross, 1941:84; Denning, 1943:144; Ross, 1944:113; Gordon, 1974:131.

Description.— Male fore-wing length 6.16 mm; chocolate-brown, not irrorate; with large paler areas near pterostigma, and about distal portions of Cu2 and A. These paler areas absent from female. Hind-wing tinted pale yellow-brown. Antennae uniformly brown except basal five flagellar annuli with oblique, darker bands; darker in female. Vertex dark chocolate-brown; darker in female. Spurs pale grey-brown; except latero-apical spur of fore-leg hyaline, finer, shorter than mesal companion. Female fore-leg latero-apical spur not hyaline, but finer, shorter than mesal companion. Thorax dark chocolate-brown, to deep red-brown laterally. Legs pale red-brown.

Genitalia. Male. (Fig. 75–78). (Specimen from Huberdeau, Québec). Males distinguished by darkly sclerotised cross-shaped pattern which links segment IX with tergum X (Fig. 75); by distal article of clasper very thin in lateral aspect, curved dorsad (Fig. 76); and by thin, high distal lobes of tergum X with deep, narrow cleft between them and main body of tergum X (Fig. 75) – these lobes close to each other in posterior aspect.

Genitalia. Female. (Fig. 79–80). (Specimen from Huberdeau, Québec). Females differentiated by clasper receptacle, in lateral aspect (Fig. 80), slightly tapered distally; by evident inner opening; by angular incision of clasper receptacle outer margin directed antero-dorsad; and by small, thin, distally little-widened sclerotised strap of vulval scale.

Biology.— Neves (1979) records from Massachusetts give a flight season of May to August, no peak mentioned. Ross (1944) indicates that this species prefers faster streams; his two Illinois records indicate that larvae also inhabit larger, slow-flowing rivers. Gordon & Wallace (1975) give major larval habitat as fallen trees and branches in flowing waters.

Distribution.— Presently recorded from Oregon, in a narrow zone across northern United States, then east to Québec and Maine, and south to Oklahoma and Florida (Map 12). In Canada it is known only from southern Québec and southern Ontario.

Cheumatopsyche mickeli Denning
Map 13; Fig. 81–86

Cheumatopsyche mickeli Denning, 1942:50; Ross, 1944:294; Gordon, 1974:132.

Description.— Male fore-wing length 6.86 mm; pale grey-brown, no pattern. Antennae yellow-brown; basal five flagellar annuli each with oblique, dark band; basal four in female. Vertex dark chocolate-brown, warts paler. Spurs brown; lateral member of middle and hind-leg pairs shorter than mesal companions. Thorax dark brown, to paler laterally. Legs pale reddish brown.

Genitalia. Male. (Fig. 81–84). (Specimen from Twenty-mile Ck, Lake Co., Oregon, USA). Males distinguished by preanal appendage tall, narrow, bowed anterad (Fig. 81); by distal article of clasper tapered fairly abruptly distad, recurved, in lateral aspect (Fig. 82); and by distal lobes of tergum X with small, squat process anteriorly on base of lobe (Fig. 81, 84).

Genitalia. Female. (Fig. 85–86). (Specimen from Twenty-mile Ck., Lake Co., Oregon, USA). Females distinguished by clasper receptacle set very high on lateral wall of segment X (Fig. 86); by inner opening evident in lateral aspect; by incision of outer margin largish, rounded; and by sclerotised strap of vulval scale inverted-triangular in lateral aspect (Fig. 86), saddle-like over dorsum of scale, not in contact with basal angle of segment X.

Biology.— Anderson's few records for Oregon indicate a flight season from at least early June to early September. Nothing more known.

Distribution.— Not yet known from Canada, this species is patchily recorded from México to Oregon, Idaho, and Wyoming (Map 13).

Cheumatopsyche campyla Ross
Map 14; Fig. 87–92

Cheumatopsyche campyla Ross, 1938b:152; Denning, 1943:148; Ross, 1944:113; Gordon, 1974:130; Schmid, 1980:144-149.

Description.— Male fore-wing length 8.35 mm; light grey-brown, with general faint irroration. Hind-wing faintly tinted brown (stronger tint in female). Antennae pale yellow-brown; basal five flagellar annuli each with oblique, dark band. Vertex very dark brown. Spur pairs of middle leg with lateral members shorter than mesal companions. Thorax dark reddish brown, to dull orange-brown laterally (chocolate-brown in female). Legs pale brown to straw.

Genitalia. Male. (Fig. 87–90). (Specimen from Wandering R., Hwy 63, 3 miles S of Wandering River, Alberta). Males distinguished by very evident dorsal lobes of segment IX, in lateral aspect (Fig. 87); by tall, clavate distal lobes of tergum X, in lateral aspect (Fig. 87); by distal lobes of tergum X close together in posterior aspect (Fig. 90); and by gently tapered black band dorsally on segment IX, curved slightly postero-ventrad.

Genitalia. Female. (Fig. 91–92). (Specimen from Wandering R., Hwy 63, 3 miles S of Wandering River, Alberta). Females distinguished by inner opening of clasper receptacle evident in lateral aspect (Fig. 92); by anterior and posterior ends of outer margin of clasper receptacle at same level; and by incision of that margin large, angular, directed posterad.

Biology.— As indicated by distribution, this species appears to be ubiquitous in its habitat preferences. It is recorded from the depths of the Boreal Forest, to deep in the heart of Texas. I have Canadian records which range from creeks to the largest rivers, some of which are deep, smooth-flowing waters, others are turbulent. Flight season, based on Canadian records, ranges from May 5 to Sept. 18 (Ontario) and October 12 (both Nova Scotia and Vancouver Island). The species may be bivoltine in the southern United States. Larvae are most commonly found out of the main current, in the backwaters, *etc.* Ross (1944) indicates that larvae of this species are very tolerant of pollution.

Distribution.— Virtually throughout the Continent, south of the northern tree line (Map 14). In Canada it has been recorded from south-central British Columbia, northern Alberta, northern Québec, Labrador, Newfoundland, and points south.

Cheumatopsyche ela Denning
Map 15; Fig. 93–98

Cheumatopsyche ela Denning, 1942:50; Ross, 1944:294; Gordon, 1974:130.

Description.— Male fore-wing length 7.72 mm; overall pale red-brown. Hind-wing very palely tinted brown, with anal lobe uniform pale grey-brown. Antennae dark brown; basal five flagellar annuli with oblique, dark band. Vertex dark chocolate-brown. Spurs straw-coloured. Thorax very dark chocolate-brown, to very dark reddish brown laterally. Legs warm reddish brown.

Genitalia. Male. (Fig. 93–96). (Specimen from St Hippolyte, Québec). Males distinguished by very distinct dorsal lobes of segment IX, in lateral aspect (Fig. 93); by distal lobes of tergum X clearly separated from main body of tergum X by shallow, rounded notch; by distal lobes, in posterior aspect, close together (Fig. 95); and by tergum X clearly delimited from segment IX by marginal declivity of segment IX.

Genitalia. Female. (Fig. 97–98). (Specimen from St Hippolyte, Québec). Females distinguished by anterior end of clasper receptacle outer margin lower than posterior end (Fig. 97); by outer margin with incision angular, directed dorsad; by receptacle directed antero-dorsad; and by inner opening of receptacle not evident in lateral aspect.

Biology.— Records few, but flight season in eastern United States ranges from April to July. Roy & Harper (1979) give known flight season in southern Québec as June 25 to August 7. Little seems to be known of stream types favoured by larvae.

*Distribution.*— Scattered records from Tennessee and South Carolina to southern Québec (Map 15). To date Canadian records are all from the Ottawa–St Lawrence rivers drainage.

Map 12. Collection localities for *Cheumatopsyche pasella* Ross in Canada, with known distribution in North America by state or province.
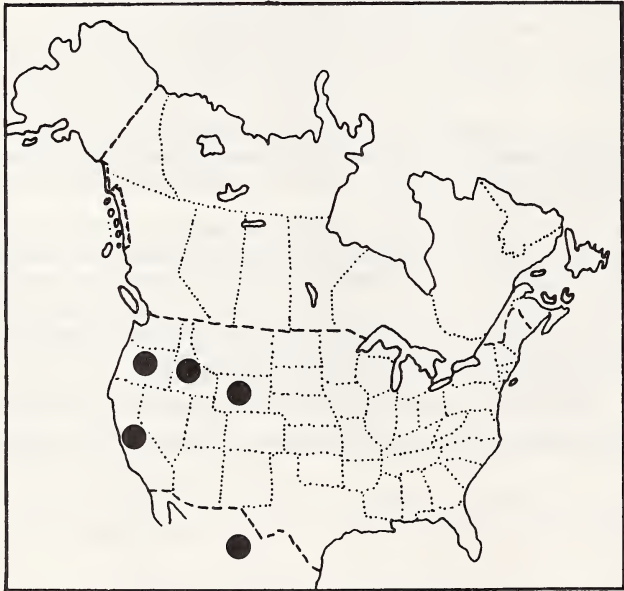
Map 13. Known distribution of *Cheumatopsyche mickeli* Denning in North America, by state.
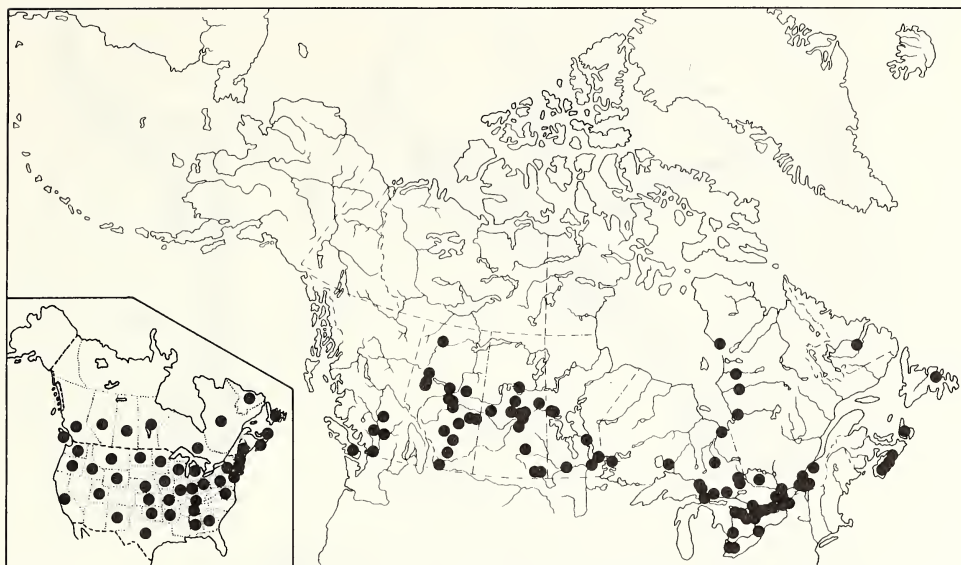
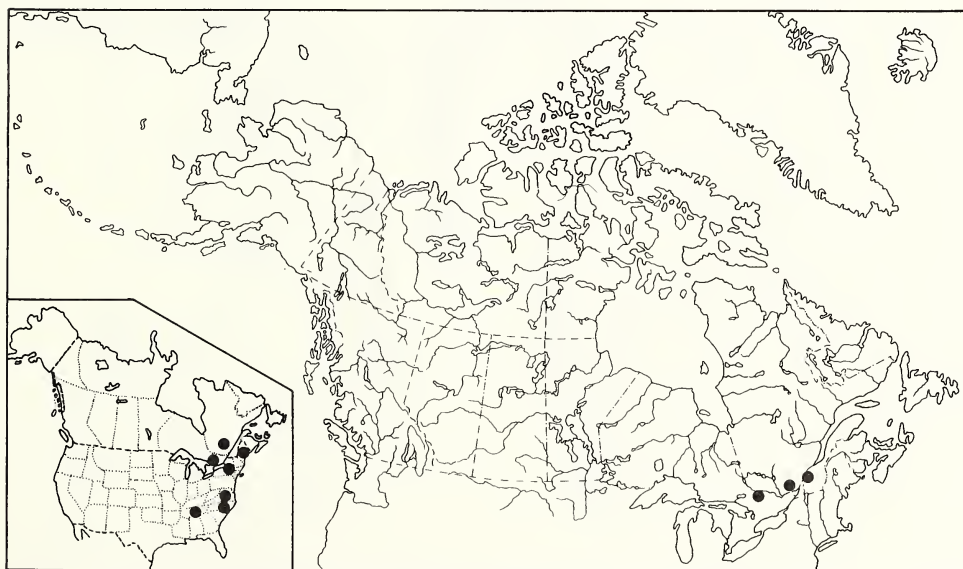Map 14. Collection localities for *Cheumatopsyche campyla* Ross in Canada, with known distribution in North America by state or province.

Map 15. Collection localities for *Cheumatopsyche ela* Denning in Canada, with known distribution in North America by state or province.

Fig. 75–80, *Cheumatopsyche pasella* Ross: 75, genital capsule of male, lateral aspect; 76, left clasper of male, posterior aspect; 77, aedeagus of male, lateral aspect; 78, segment X of male, posterior aspect; 79, genital segments of female, dorsal aspect; 80, genital segments of female, lateral aspect.

Fig. 81–86, *Cheumatopsyche mickeli* Denning: 81, genital capsule of male, lateral aspect; 82, left clasper of male, posterior aspect; 83, aedeagus of male, lateral aspect; 84, segment X of male, posterior aspect; 85, genital segments of female, dorsal aspect; 86, genital segments of female, lateral aspect.
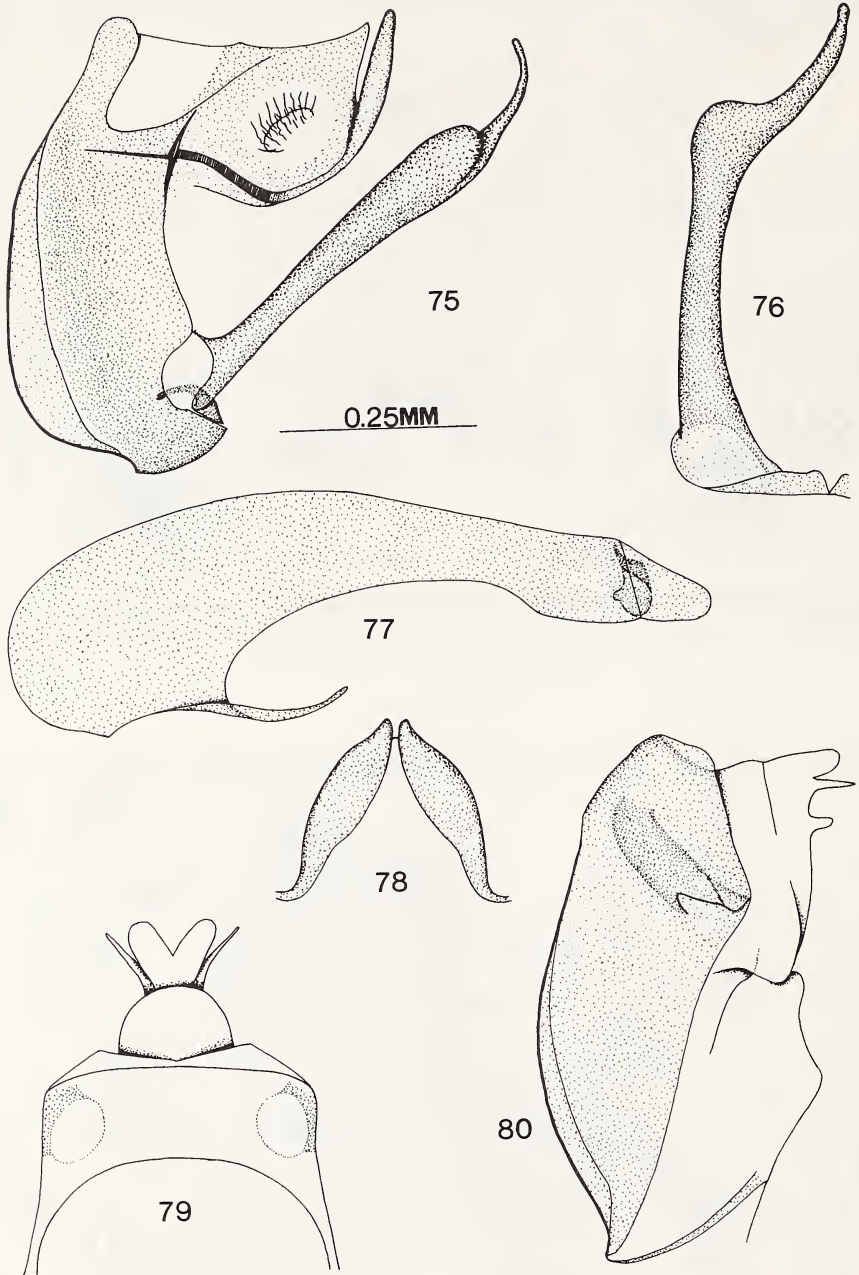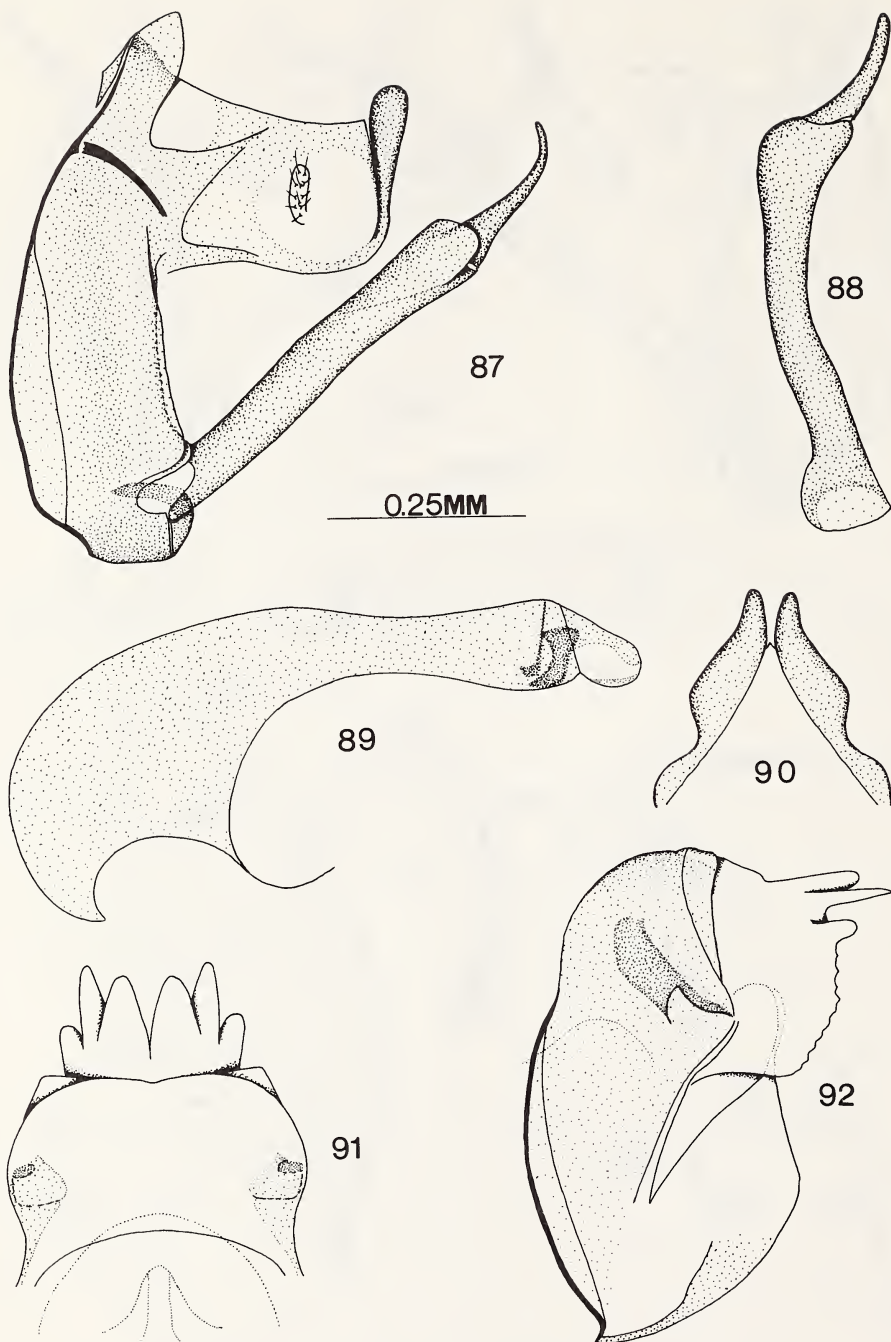
Fig. 87–92, *Cheumatopsyche campyla* Ross: 87, genital capsule of male, lateral aspect; 88, left clasper of male, posterior aspect; 89, aedeagus of male, lateral aspect; 90, segment X of male, posterior aspect; 91, genital segments of female, dorsal aspect; 92, genital segments of female, lateral aspect.
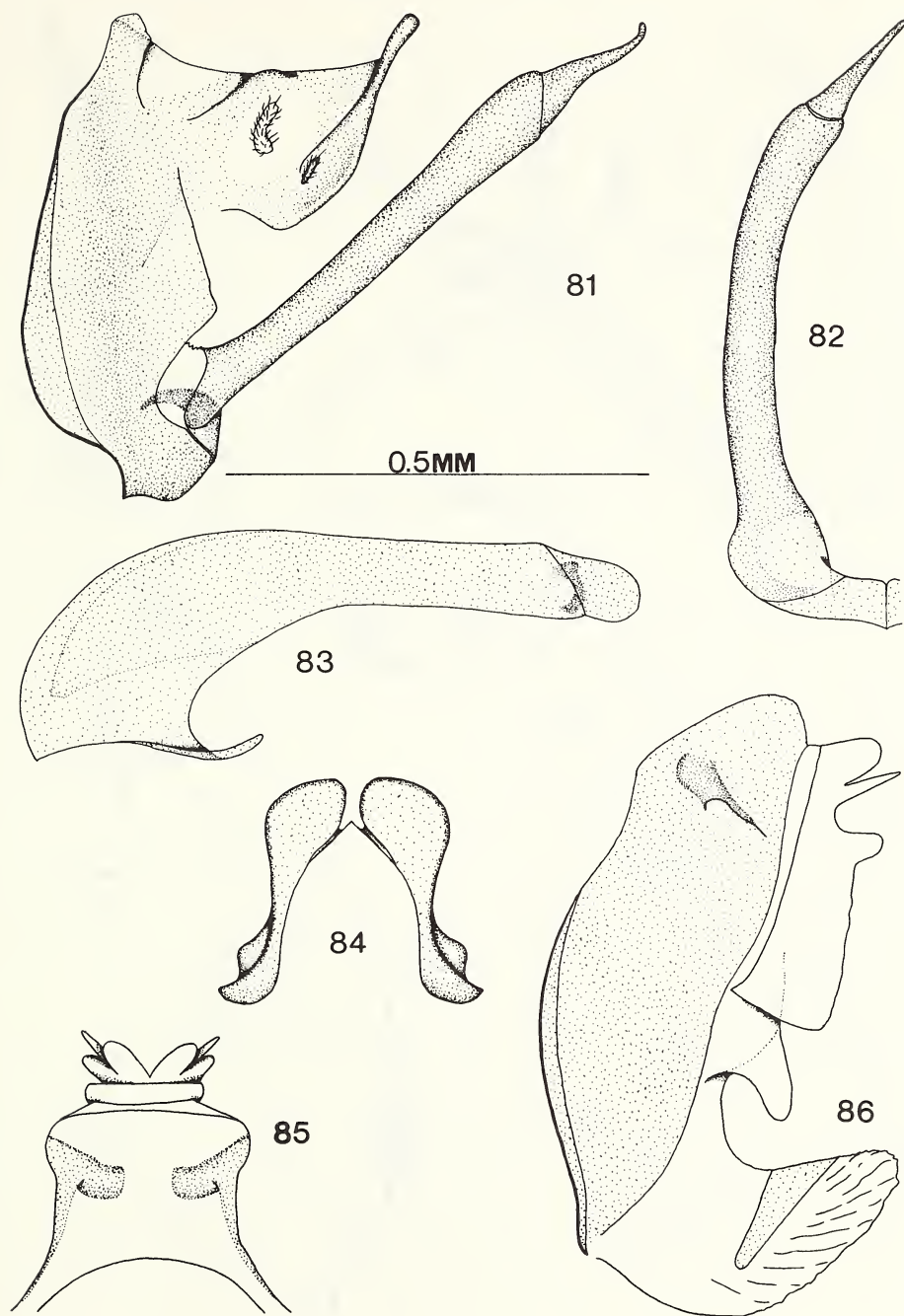
Fig. 93–98, *Cheumatopsyche ela* Denning: 93, genital capsule of male, lateral aspect; 94, left clasper of male, posterior aspect; 95, segment X of male, posterior aspect; 96, aedeagus of male, lateral aspect; 97, genital segments of female, lateral aspect; 98, genital segments of female, dorsal aspect.
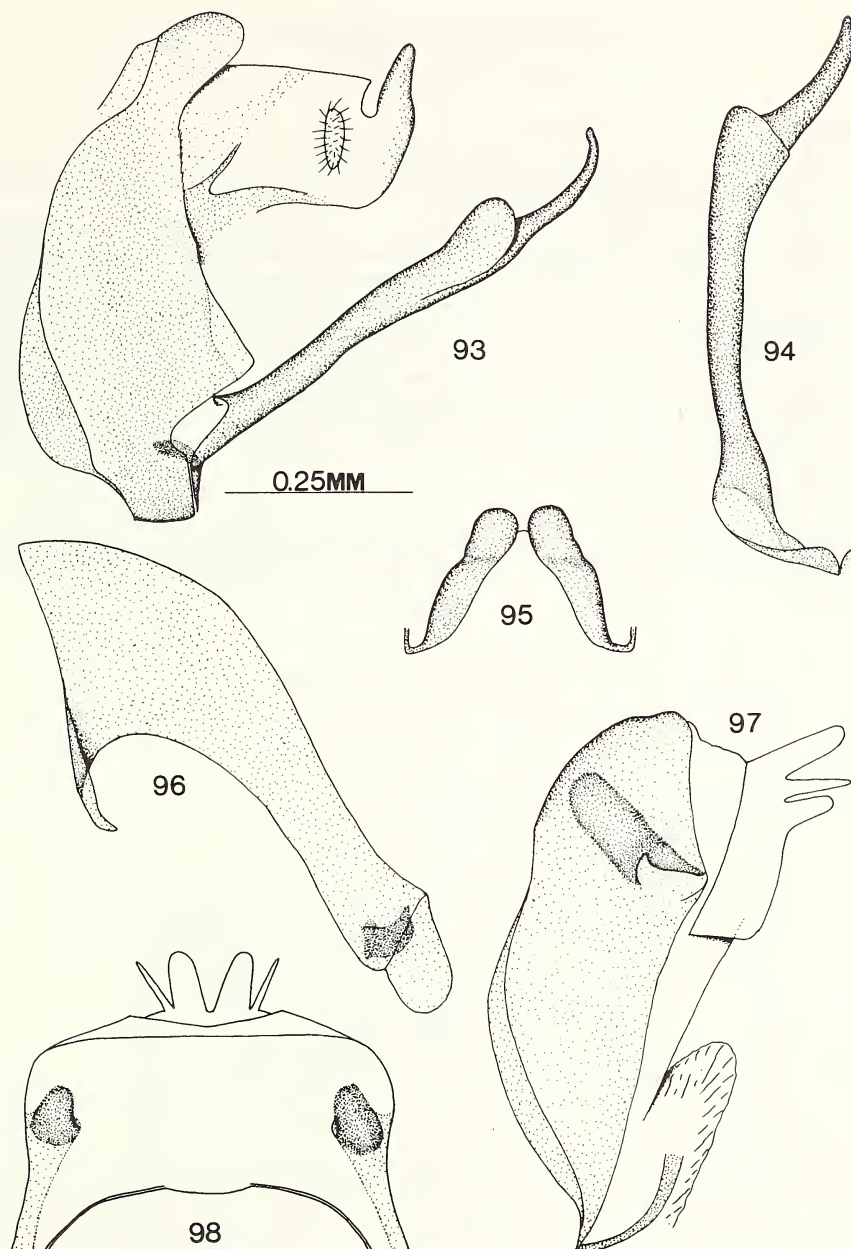
THE *WABASHA* GROUP

Cheumatopsyche wabasha Denning
Map 16; Fig. 99–102

Cheumatopsyche wabasha Denning, 1947:252; Gordon, 1974:130.

Description.— Male fore-wing length 6.7 mm; deep translucent red-brown; very faintly irrorate. Hind-wing paler, no irroration. Antennae missing; basal segment dark brown. Vertex very dark brown to chocolate. Thorax chocolate to almost black. Legs dark brown to chocolate.

Genitalia. Male. (Fig. 99–102). (Specimen from Wabasha, Minnesota, USA – Holotype). Gordon used an Oregon specimen for her illustrations of the male, and description. That specimen was apparently not deformed, as she refers to the distal deformation of the aedeagus of the male holotype (see Fig. 102 here). She makes no reference to the deformation of the distal lobes of tergum X as evinced in either lateral or posterior aspects (Fig. 99 & 100 here). Just which, if any, of the distal lobes borne by the holotype should be regarded as normal for the species is open to doubt. Gordon's illustrations of the Oregon specimen seem to show a third type of lobe (posterior aspect). Loss of tergum X distal lobes as reliable characters is unfortunate, but the holotype, and the Oregon specimens appear to agree in having dorsum of tergum X level, almost at same height as dorsal lobes of segment IX (Fig. 99). Also, the preanal appendages agree in being located almost on the base of the distal lobes. The distal article of the clasper is very narrow throughout, in lateral aspect, and sharply hooked dorsad at distal end; in posterior aspect (Fig. 101) clasper distal article curved posterad, with relatively wide base, distally acuminate.

Genitalia. Female. Unknown.

Biology.— Unknown except that both Minnesota and Oregon adult records are for July.

Distribution.— Presently known only from Minnesota and Oregon, in the United States (Map 16).

Map 16. Known distribution of *Cheumatopsyche wabasha* Denning in North America, by state.
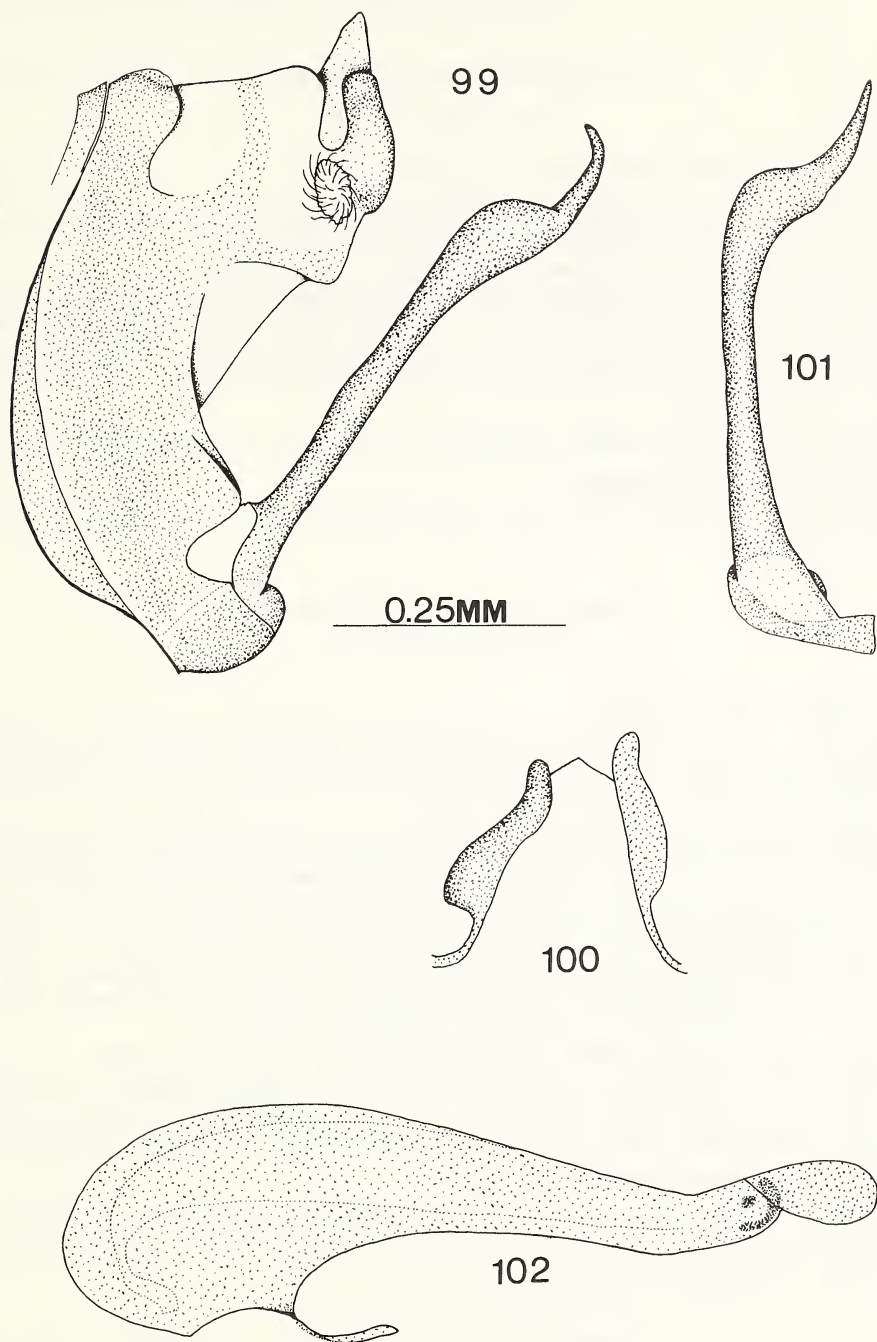
Fig. 99–102, *Cheumatopsyche wabasha* Denning: 99, genital capsule of male, lateral aspect; 100, segment X of male, posterior aspect; 101, left clasper of male, posterior aspect; 102, aedeagus of male, lateral aspect.

THE *ROSSI* GROUP

Cheumatopsyche logani Gordon & Smith
Map 18; Fig. 103–106

Cheumatopsyche logani Gordon & Smith, 1974:1; Gordon, 1974:128.

Description.— Male fore-wing length 6.94 mm; pale brownish cream; no evident pattern – may be teneral. Antennae pale straw, no markings on flagellar annuli; scape brown, with cream-coloured areas baso-laterad; pedicel brown, with posterior area cream. Vertex red-brown, warts almost white. Legs straw-coloured.

Genitalia. Male. (Fig. 103–106). (Specimen from Little Salmon R., Adams Co., Idaho, USA – Holotype). Males distinguished by distal article of clasper with basal half evenly tapered; distal half uniformly thin, curved dorso-anterad, in lateral aspect (Fig. 103). Distal article of clasper, in posterior aspect, directed postero-mesad, with tip just visible, directed mesad (Fig. 105). Dorsum of tergum X sloped postero-ventrad directly from dorsum of segment IX. Preanal appendage globular, close to base of tergum X distal lobes. Distal lobes of tergum X separated from main body of tergum by shallow, narrowly v-shaped notch; close together in posterior aspect (Fig. 104).

Genitalia. Female. Unknown.

Biology.— The only flight records available are June 3 and 29, in Washington and Idaho respectively. Otherwise nothing known.

Distribution.— Presently recorded only from Washington, Idaho, and Montana, in the United States (Map 18).

Cheumatopsyche smithi Gordon
Map 19; Fig. 107–112

Cheumatopsyche smithi Gordon, 1974:128.

Description.— Male fore-wing length 8.42 mm; warm golden brown; paler areas only at distal end of A. Female more distinctly irrorate. Antennae brown; basal six flagellar annuli with oblique, dark brown bands; dark yellowish brown in female. Spurs brownish yellow; lateral member of middle leg pairs notably shorter than mesal companions. Thorax dark reddish brown, to greyish brown laterally. Legs pale yellowish brown.

Genitalia. Male. (Fig. 107–110). (Specimen from Wandering R., Hwy 63, N of Wandering River, Alberta). Males distinguished by basal article of clasper very stout, expanded evenly distad, extended dorsad of tergum X; by distal article of clasper minute by comparison with basal article, tapered distad to fine point, recurved; by distinct dorsal lobes of segment IX (Fig. 107); by distal lobes of tergum X well separated from main body of tergum X by narrow cleft, in lateral aspect (Fig. 110), with dorsal portion expanded, rounded, flared dorso-laterad; and by small, circular preanal appendages.

Genitalia. Female. (Fig. 111–112). (Specimen from Wandering R., Hwy 63, N of Wandering River, Alberta). Females distinguished by clasper receptacle expanded distally, in lateral aspect (Fig. 112), with inner end very slightly cleft; by outer margin of receptacle incised, rounded, incision located at anterior end of margin; by receptacle directed postero-dorsad; and by sclerotised strap of vulval scale narrow, tapered to fine point distally.

Biology.— Flight season records for Canada range from May 18 to August 12, with imprecisely defined concentration in June and July. Larvae appear to inhabit a variety of stream types, from smaller creeks to large rivers, and slower deep waters to fast-flowing waters on gravel or boulder beds. Records are available from the Vancouver Island rain forest, the Boreal Forest, prairies, and far southern Ontario.

Distribution.— Recorded to date from Vancouver Island and southern British Columbia, to southern Ontario, and three States of the Union adjacent to the Canadian border (Map 19). In Canada most records are from Alberta.

Cheumatopsyche pettiti (Banks)
Map 17; Fig. 113–118

Hydropsyche pettiti Banks, 1908:265; Milne, 1936:73 (with *H. analis* Banks as synonym of *H. morosa*).
Hydropsychodes pettiti; Betten, 1934:195.
Cheumatopsyche pettiti; Knowlton & Harmston, 1938:285; Denning, 1943:145; Ross, 1944:294 (as synonym of *C. analis*

Nimmo, A. P. (1987, 1–189).– The adult Arctopsychidae and Hydropsychidae (Trichoptera) of Canada and adjacent United States

CORRIGENDA

pages

49   "(Fig. 17)" in the last paragraph should read "(Map 17)".

49–50   Captions for maps are in correct places but maps should be rearranged as
         follows:

Map at	should go to
17	18
19	17
18	19

Banks); Gordon, 1974:127, 143 (*C. analis* as *nomina dubia*).
Hydropsyche analis Banks, 1903:243; Milne, 1936:73 (as synonym of *H. morosa*); Ross, 1944:112.
*Hydropsychodes analis*; Betten, 1934:194.

Description.— Male fore-wing length 7.41 mm; pale grey-brown. Hind-wing hyaline. Antennae brown; basal four flagellar annuli with oblique, dark band; basal five annuli in female. Vertex deep red-brown. Spurs brown; lateral member of fore-leg pair finer than mesal companion, hyaline; lateral member of middle leg sub-apical pair shorter than mesal companion. Thorax deep red-brown, to paler laterally. Legs dark straw-coloured.

Genitalia. Male. (Fig. 113–116). (Specimen from R. Maskinonge, Ste Angèle, Québec). Males distinguished by distal lobes of tergum X very well separated from main body of tergum X, in lateral aspect (Fig. 113); by distal lobes of tergum X, in posterior aspect (Fig. 116), not particularly close to each other, widened distally, with distal ends flared somewhat laterad; by dorsal lobes of segment IX clearly evident; and by distal article of clasper more or less confluent with basal article, in posterior aspect (Fig. 114).

Genitalia. Female. (Fig. 117–118). (Specimen from R. Maskinonge, Ste Angèle, Québec). Females distinguished by clasper receptacle directed antero-dorsad, in lateral aspect (Fig. 118); by outer margin of receptacle not incised, continued anterad on lateral face of segment X by thin, black line; by inner opening of clasper receptacle not evident in lateral aspect; and by sclerotised strap of vulval scale located well away from segment X, basally thin, distally greatly expanded to poorly sclerotised area which extends from dorsal to ventral regions of scale.

Biology.— Anderson (1976) summarizes present knowledge of the species. Larvae appear to prefer smaller streams, but are also recorded from larger rivers. First adults to emerge are very dark, followed by successively lighter individuals as season progresses. Flight season based on Canadian records ranges from May 11 to October 13, with no pronounced peak.

Distribution.— Known from across North America (Fig. 17), and from northern reaches of the Boreal Forest south to Texas. Apparently not yet recorded from the southeastern United States. In Canada this species is known from northern British Columbia, the western and eastern shores of Hudson's Bay, Newfoundland, and points south to the United States border. It appears that this species has also been introduced to Hawaii.
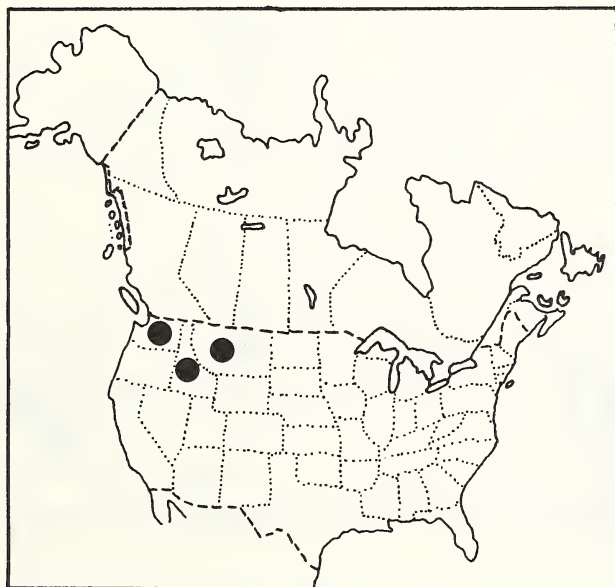
Map 17. Collection localities for *Cheumatopsyche pettiti* (Banks) in Canada, with known distribution in North America by state or province.

Map 18. Known distribution of *Cheumatopsyche logani* Gordon in North America, by state.
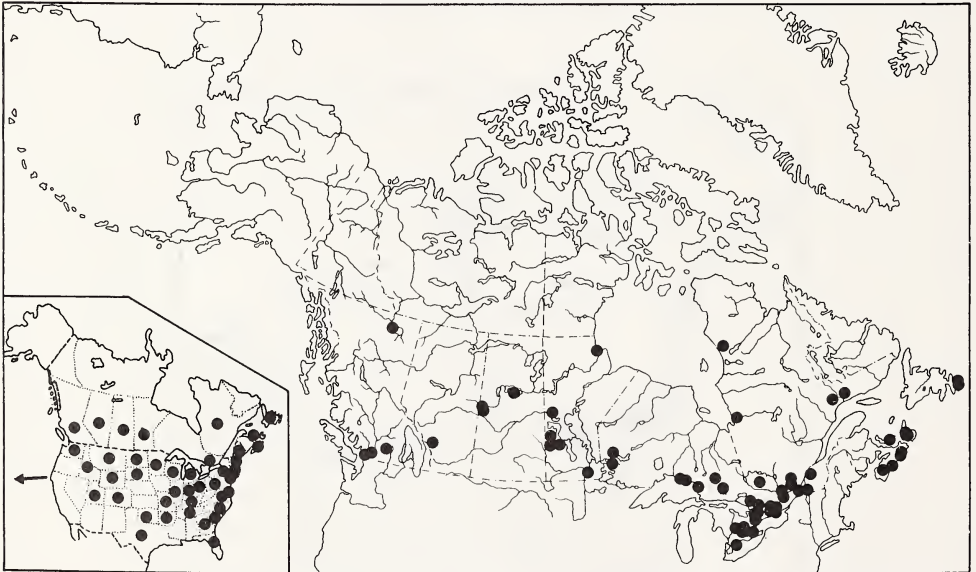
Map 19. Collection localities for *Cheumatopsyche smithi* Gordon in Canada, with known distribution in North America by state or province.
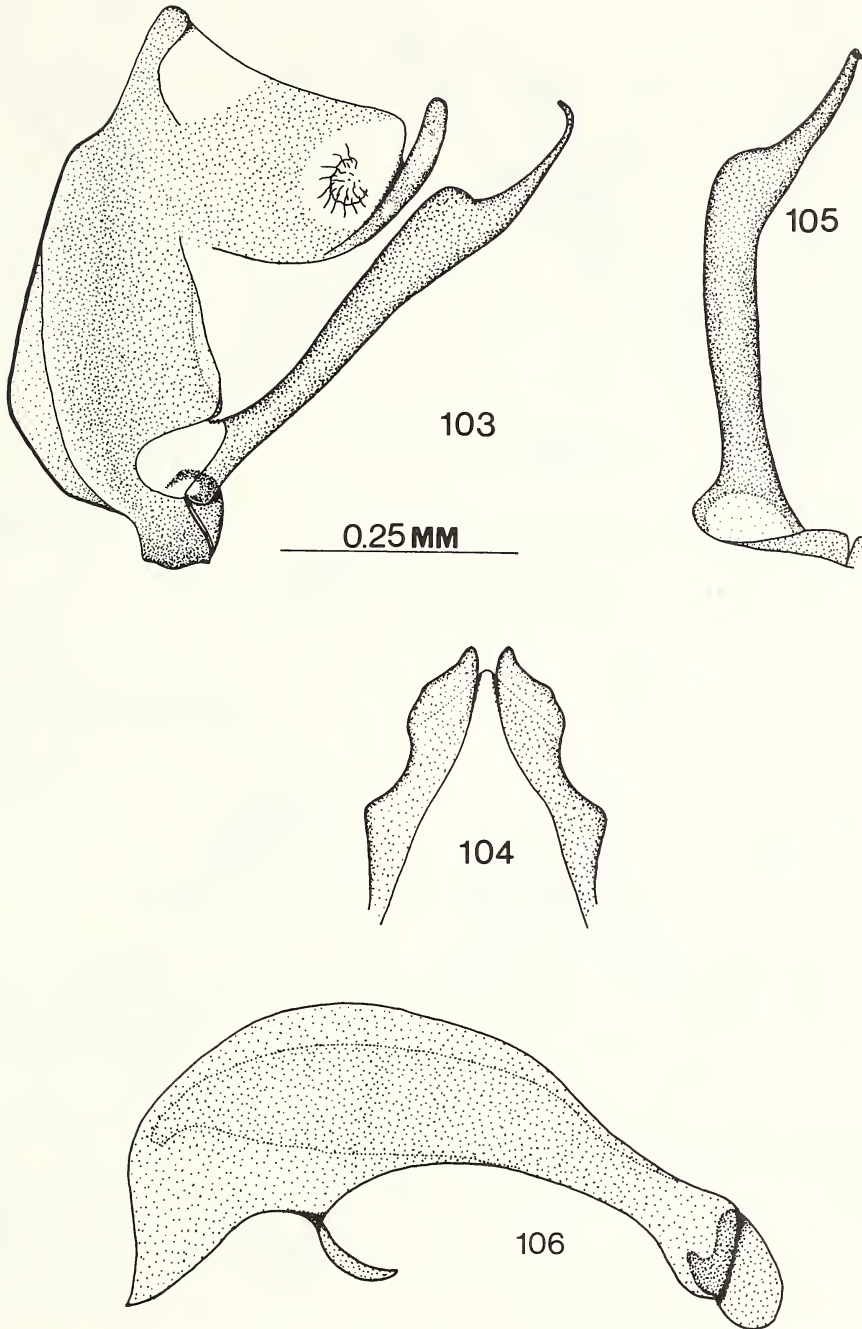
Fig. 103–106, *Cheumatopsyche logani* Gordon: 103, genital capsule of male, lateral aspect; 104, segment X of male, posterior aspect; 105, left clasper of male, posterior aspect; 106, aedeagus of male, lateral aspect.

Fig. 107–112, *Cheumatopsyche smithi* Gordon: 107, genital capsule of male, lateral aspect; 108, left clasper of male, posterior aspect; 109, aedeagus of male, lateral aspect; 110, segment X of male, posterior aspect; 111, genital segments of female, dorsal aspect; 112, genital segments of female, lateral aspect.
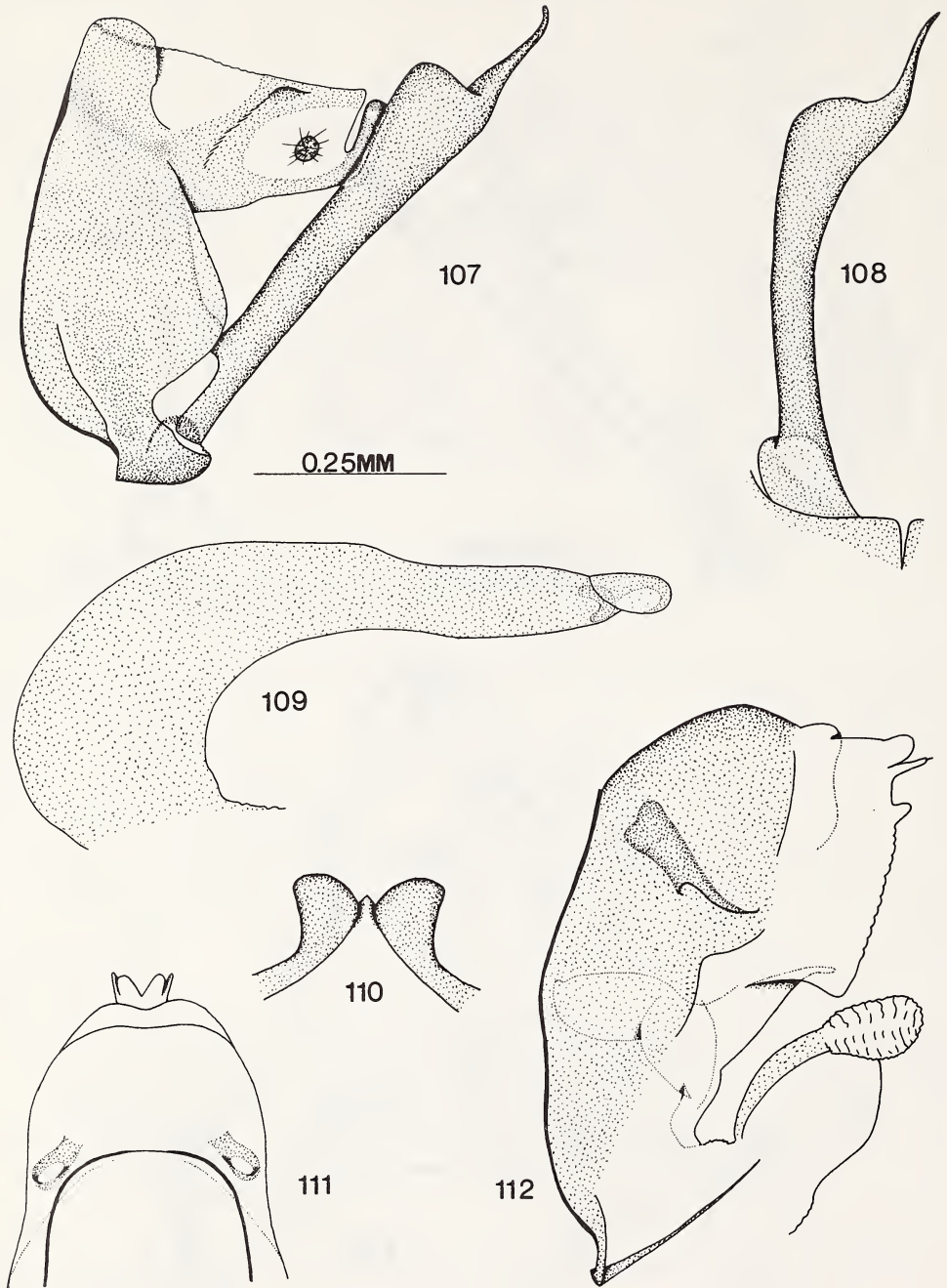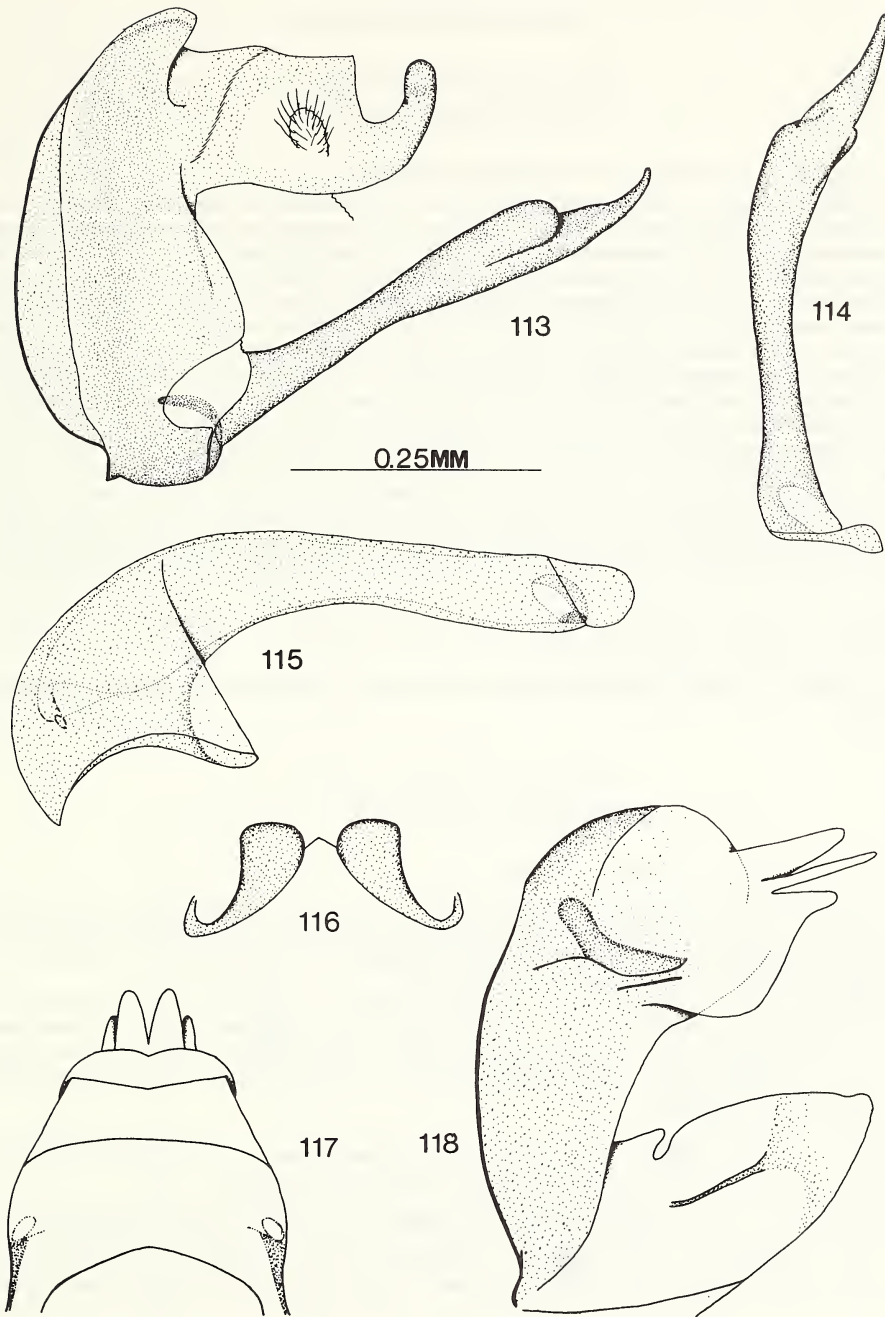
0.25MM

113

114

115

116

117   118

Fig. 113–118, *Cheumatopsyche pettiti* (Banks): 113, genital capsule of male, lateral aspect; 114, left clasper of male, posterior aspect; 115, aedeagus of male, lateral aspect; 116, segment X of male, lateral aspect; 117, genital segments of female, dorsal aspect; 118, genital segments of female, lateral aspect.

THE *HELMA* GROUP

Cheumatopsyche helma Ross
Map 20; Fig. 119–124

Cheumatopsyche helma Ross, 1939:68; Ross; 1944:294; Gordon, 1974:135.

Description.— Male fore-wing length 5.03 mm; overall warm, deep red brown; no evident pattern. Antennae brown; basal five flagellar annuli each with oblique, faintly darker band. Vertex uniform dark brown. Spurs dark brown; lateral member of middle leg pairs shorter than mesal companions; lateral member of front leg apical pair minute, hyaline (normal in female). Thorax dark brown, to dull grey-brown laterally. Legs brownish yellow.

Genitalia. Male. (Fig. 119–122). (Specimen from Pineville, Kentucky, USA – Paratype). Males distinguished by dorsal lobes of segment IX (Fig. 119); by small preanal appendage about mid-point along length of tergum X; by distal lobes of tergum X, in lateral aspect, triangular, antero-dorsal corner directed anterad; by distal lobes of tergum X, in posterior aspect, clearly separated by higher, intermediate, angular roof of tergum (Fig. 120); by distal lobes with acuminate dorso-lateral lobes, in posterior aspect, directed laterad; by segment IX tall, narrow in lateral aspect, with no posterior projection of postero-lateral edge (compare Fig. 119 & 113); and by distal article of clasper much thinner than basal article, almost straight in lateral and posterior aspect (Fig. 119, 121), with little taper.

Genitalia. Female. (Fig. 123–124). (Specimen from Gatlinburg, Tennessee, USA). Females distinguished by very large clasper receptacle, in lateral aspect (Fig. 124), curved dorso-posterad, of uniform width; by inner opening of clasper receptacle not evident in lateral aspect; by outer margin of receptacle incised at anterior end – incision minute, narrow, short, directed dorsad; by anterior end of outer margin of receptacle continued by, but not connected to, thin, dark line across lateral face of segment X; and by large sclerotised strap of vulval scale, with dorsal area of sclerotisation also present.

Biology.— Blickle & Morse (1966) record adult collection dates from July 8 to 30, in Maine. Nothing more known at present.

Distribution.— Presently known only from Tennessee, Kentucky, and Maine, in the USA (Map. 20).

Cheumatopsyche wrighti Ross
Map 21; Fig. 125–128

Cheumatopsyche wrighti Ross, 1947:140; Gordon, 1974:136.

Description.— Male fore-wing length 7.87 mm; uniform warm red-brown; no evident pattern. Antennae brown; basal five flagellar annuli each with oblique, dark band. Vertex deep red-brown, warts paler. Spurs straw-coloured; lateral spurs of all pairs on middle and hind legs noticeably shorter than mesal companions. Thorax rich, deep red-brown, to partly greyish brown laterally. Legs light red-brown, to paler distally.

Genitalia. Male. (Fig. 125–128). (Specimen from Camp Ck, Greene Co., Tennessee, USA – Holotype). Males distinguished by distal lobes of tergum X very large, appressed anterad along lateral face of tergum X, in lateral aspect (Fig. 125); by distal lobes of tergum X with posterior edge, in lateral aspect, shouldered; by total lack of dorsal lobes of segment IX; by distal lobes of tergum X close in posterior aspect (Fig. 126), tapered dorso-mesad; and by recurved distal article of clasper in posterior aspect (Fig. 127).

Genitalia. Female. Unknown.

Biology.— Neves (1979) records adults from Massachussetts in June-July. The only Canadian records are from July 5 and 11. Nothing else presently known.

Distribution.— In the United States this species is recorded from Tennessee and the northeastern seaboard states (Map 21). In Canada there are two records: from Baddeck, Cape Breton Island, Nova Scotia, and from near Dundee in the eastern half of Prince Edward Island.

Cheumatopsyche h. harwoodi Denning
Map 22; Fig. 129–134

Cheumatopsyche harwoodi Denning, 1949:41.
Cheumatopsyche h. harwoodi; Gordon, 1974:135.

Of the two subspecies recognised by Gordon (1974) *C. h. harwoodi* is the one most likely to be recorded from Canada.

Description.— Male fore-wing length 6.79 mm; grey-brown. Hind-wing palely tinted grey-brown. Antennae dark brown; basal six flagellar annuli each with oblique, dark band. Vertex chocolate; posterior warts paler. Spurs dark brown; lateral member of middle leg pairs much shorter than mesal companions. Thorax chocolate, to mixed chocolate and paler laterally. Legs dull yellowish brown.

Genitalia. Male. (Fig. 129–132). (Specimen from Credit R., Belfountain, Halton Co., Ontario). Males distinguished by lack of dorsal lobes on segment IX (Fig. 129); by preanal appendage vertically aligned, small, narrowly elliptical; by small, rounded notch between main body of tergum X and distal lobes; by distal lobes of tergum X, in lateral aspect (Fig. 129), slightly higher than tergum X, widest dorsally; by distal lobes of tergum X, in posterior aspect (Fig. 131), moderately separated, with dorso-lateral corners right-angled, and dorso-mesal corners rounded, produced slightly dorsad; and by basal article of clasper, in posterior aspect (Fig. 130), distally curved gently mesad, with distal half much wider – distal article of clasper with base narrower than distal end of basal article, gently curved dorsad, tapered to thin, rounded tip.

Genitalia. Female. (Fig. 133–134). (Specimen from Credit R., Belfountain, Halton Co., Ontario). Females distinguished by clasper receptacle of medium size, directed dorso-anterad in lateral aspect (Fig. 134), without inner opening evident; by outer margin of receptacle with deep, angular incision directed dorsad; by anterior end of outer margin continued antero-ventrad across lateral face of segment IX by thin, black, sinuate line; by sclerotised strap of vulval scale short, very thin; and by cercus of segment XI very small, short, thin, located immediately at base of dorsal lobe of segment XI.

Biology.— Flight season data very scarce in literature, but McElravy & Foote (1978) record possible females from Ohio on August 5. Denning's original material from Tennessee was collected on June 6. I have two records from eastern Canada – July 11 and 16. Nothing else known.

Distribution.— Known from most eastern states of the Union, north of Florida and Alabama, as far as Maine (Map 22). In Canada the species has been taken in Nova Scotia and Prince Edward Island.
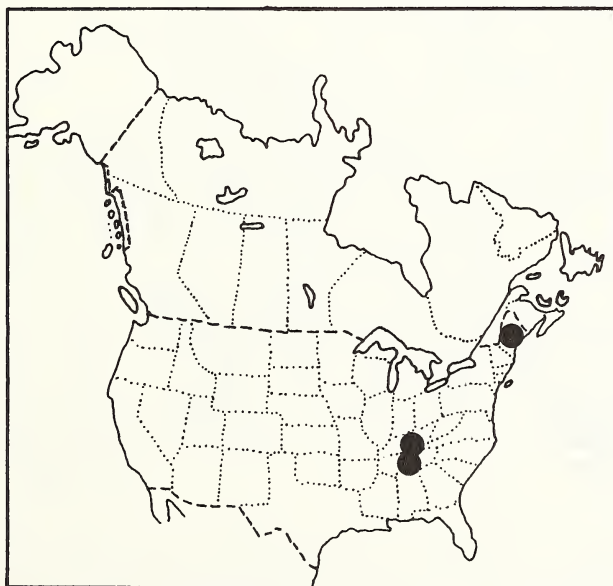
Map 20. Known distribution of *Cheumatopsyche helma* Ross in North America, by state.
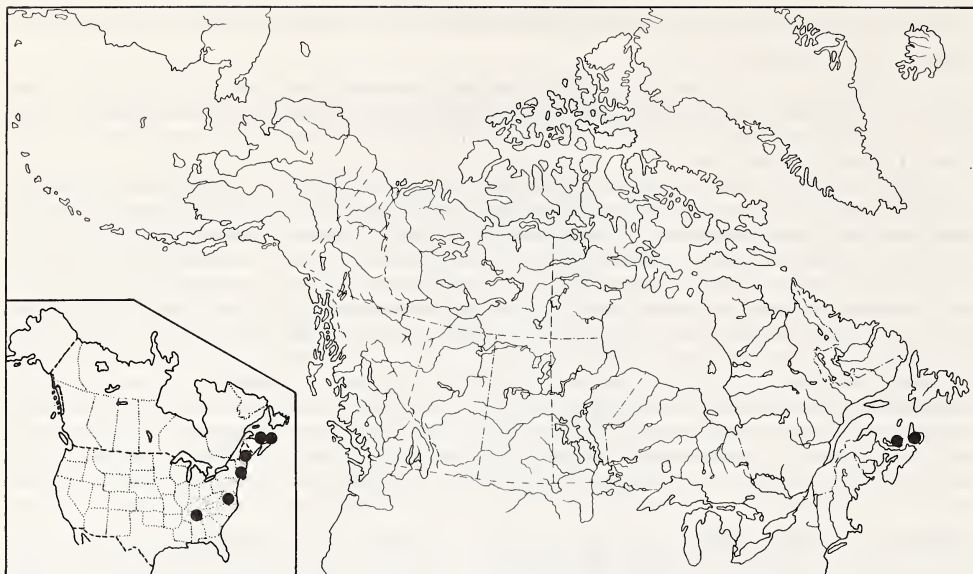
Map 21. Collection localities for *Cheumatopsyche wrighti* Ross in Canada, with known distribution in North America by state or province.
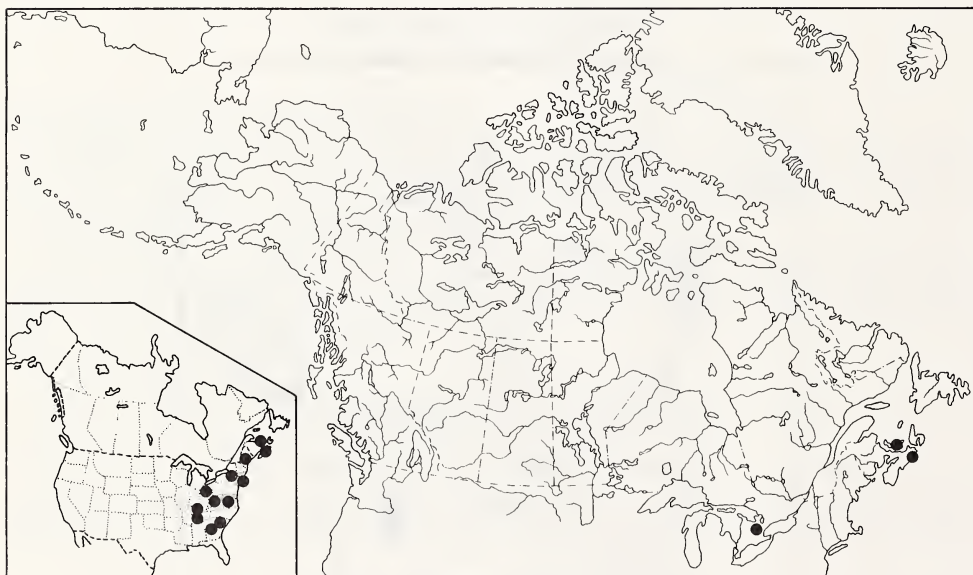
Map 22. Collection localities for *Cheumatopsyche h. harwoodi* Denning in Canada, with known distribution in North America by state or province.
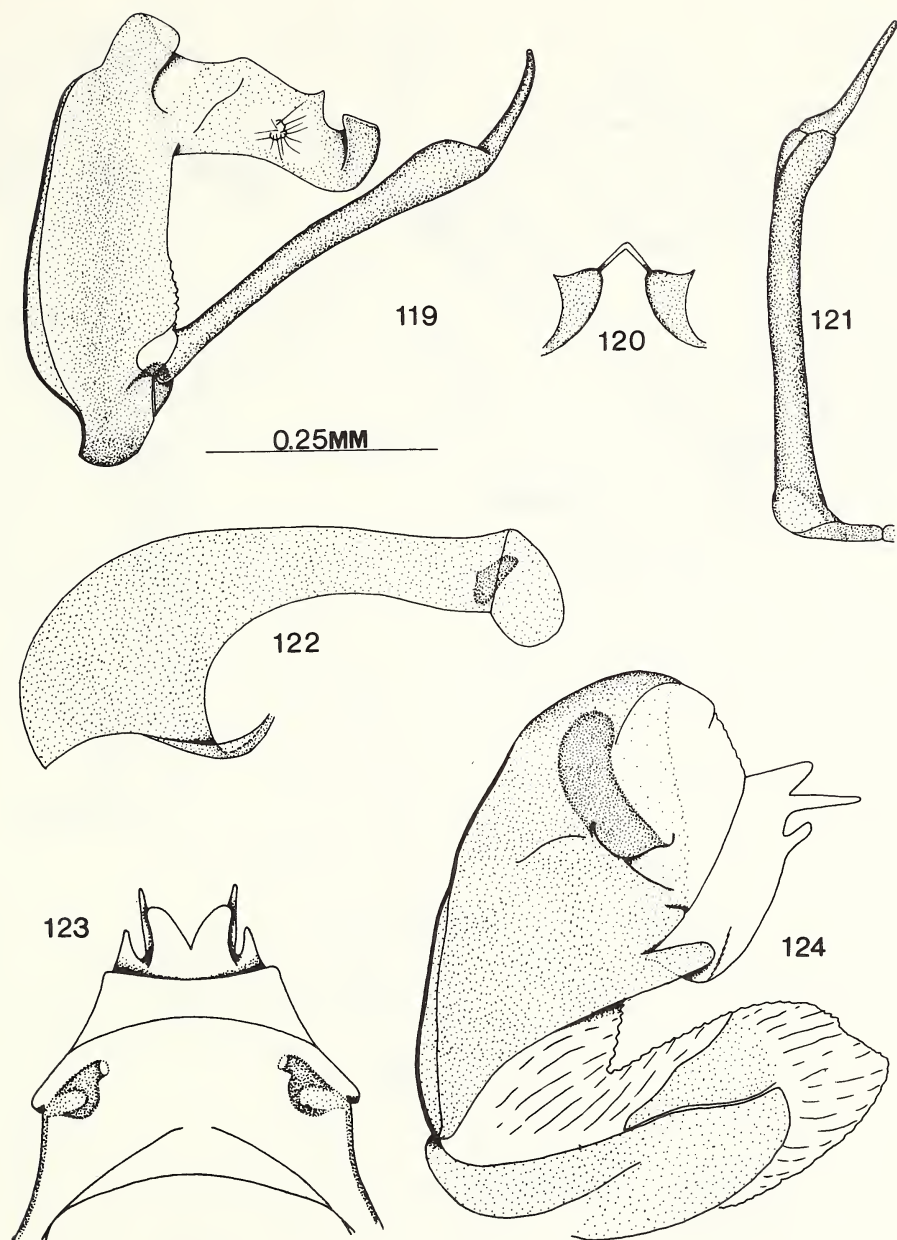
Fig. 119–124, *Cheumatopsyche helma* Ross: 119, genital capsule of male, lateral aspect; 120, segment X of male, posterior aspect; 121, left clasper of male, posterior aspect; 122, aedeagus of male, lateral aspect; 123, genital segments of female, dorsal aspect; 124, genital segments of female, lateral aspect.
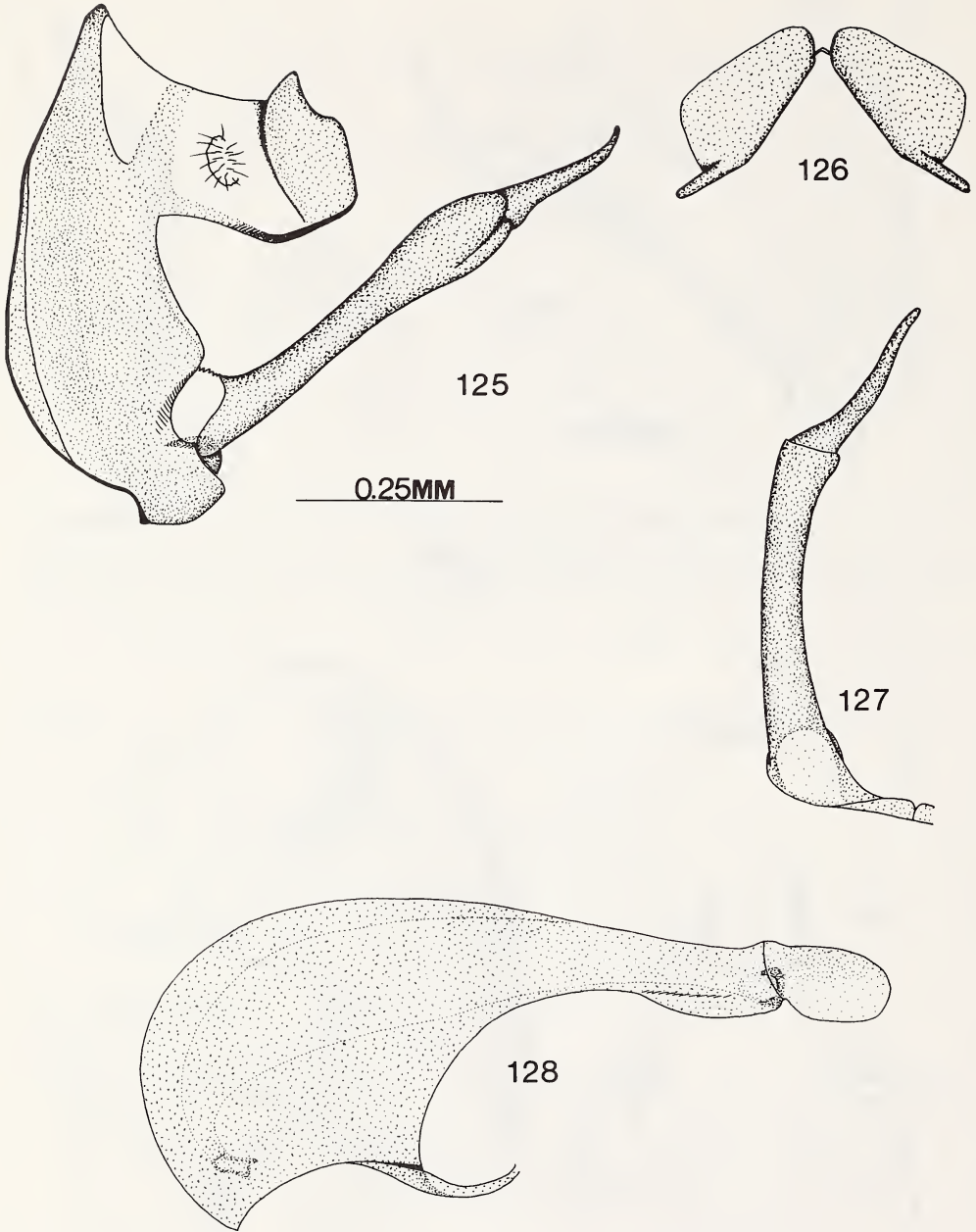
Fig. 125–128, *Cheumatopsyche wrighti* Ross: 125, genital capsule of male, lateral aspect; 126, segment X of male, posterior aspect; 127, left clasper of male, posterior aspect; 128, aedeagus of male, lateral aspect.
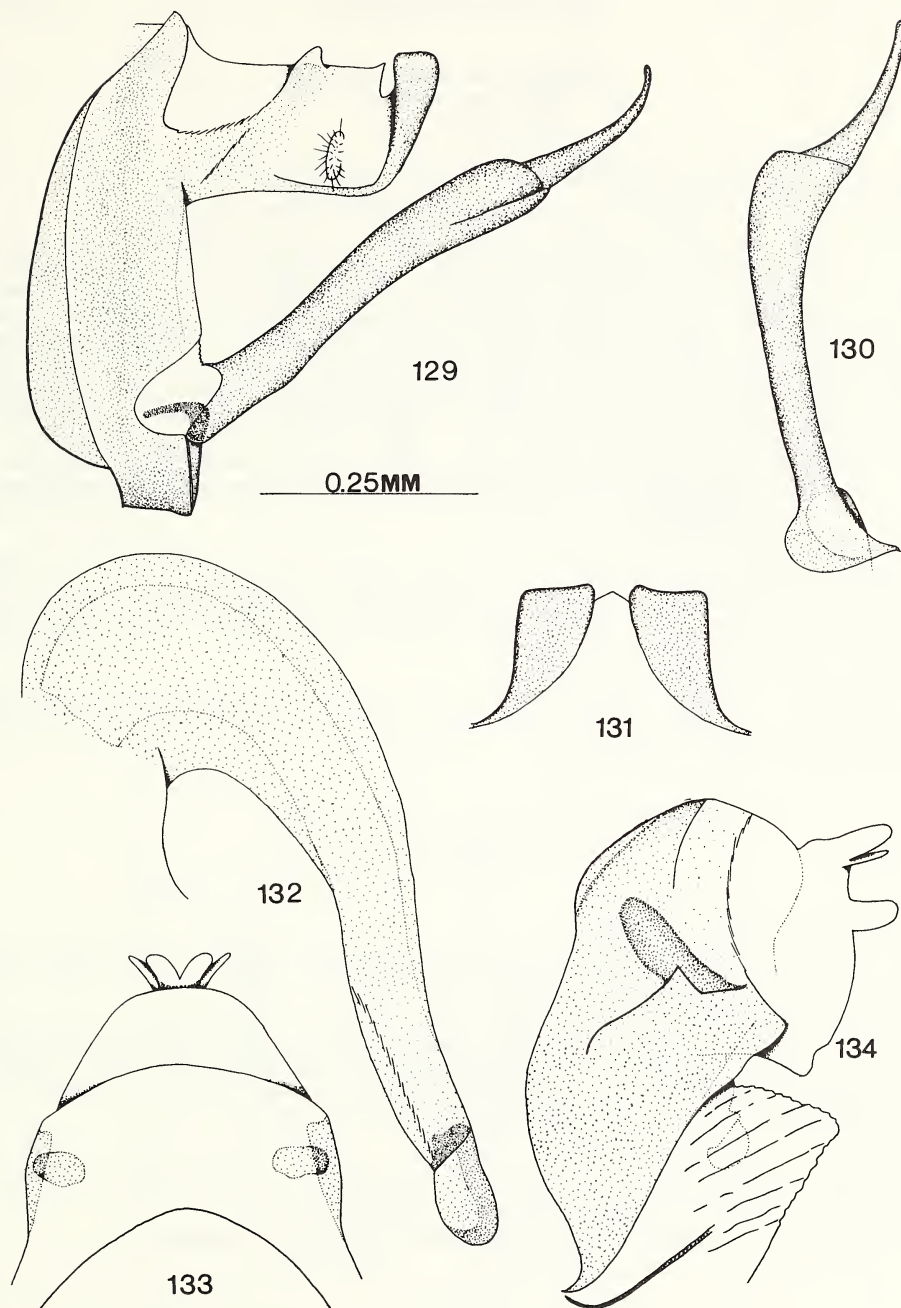
Fig. 129–134, *Cheumatopsyche h. harwoodi* Denning: 129, genital capsule of male, lateral aspect; 130, left clasper of male, posterior aspect; 131, segment X of male, posterior aspect; 132, aedeagus of male, lateral aspect; 133, genital segments of female, dorsal aspect; 134, genital segments of female, lateral aspect.

THE *GRACILIS* GROUP

Cheumatopsyche gracilis (Banks)
Map 23; Fig. 135–140

Hydropsyche gracilis Banks, 1899:216; Milne, 1936:73 (as synonym of *H. morosa*).
Hydropsychodes gracilis; Betten, 1934:197.
Cheumatopsyche gracilis; Ross, 1938c:15; Denning, 1943:152; Ross, 1944:294; Gordon, 1974:137.

Description.— Male fore-wing length 6.16 mm; pale yellow-brown, with faint, scattered pattern. Antennae yellow-brown; basal five flagellar annuli each with oblique, dark brown band. Spurs yellow-brown; lateral member of middle leg pairs notably shorter than mesal companions. Thorax dark brown, to paler laterally. Legs pale yellow-brown.

Genitalia. Male. (Fig. 135–140). (Specimen from Waterton R., nr Standoff, Alberta). Males distinguished by lack of dorsal lobes on segment IX (Fig. 135); by tergum X sloped postero-ventrad; by preanal appendage large, ovoid; by distal lobes of tergum not separated from tergum X by gap, in lateral aspect (Fig. 135), antero-dorsal corner angular, turned slightly dorsad; by distal lobes of tergum X, in posterior aspect (Fig. 137), clearly separated, roughly triangular, with dorso-lateral corners directed dorso-laterad; and by entire clasper, in posterior aspect (Fig. 136), recurved as unit, without apparent distinction between basal and distal articles.

Genitalia. Female. (Fig. 139–140). (Specimen from Waterton R., nr Standoff, Alberta). Females distinguished by massive clasper receptacle (Fig. 140); outer margin of receptacle sinuate, produced ventrad as large, rounded lobe; by anterior end of outer margin of receptacle continued shortly antero-ventrad as black line; and by receptacle as whole located very high in segment IX, almost to dorsal crest.

Biology.— Recorded from northern reaches of Boreal Forest, south almost to Texas. Available records indicate that larvae inhabit a wide range of stream types, from small to very large, slow to fast and turbulent. Flight season ranges from at least May 12 to August 30 in Canada, with possible peak in June-July.

Distribution.— Trans-continental, recorded from Boreal Forest south to Utah, Arkansas, and North Carolina (Map 23). In Canada this species is recorded from south-central British Columbia to Labrador and Nova Scotia.

Cheumatopsyche vannotei Gordon
Map 24; Fig. 141–144

Cheumatopsyche vannotei Gordon, 1974:138.

Description.— Male fore-wing length 7.02 mm; yellowish brown, evenly irrorate. Hind-wing palely tinted brown. Antennae brown basally, to light yellow-brown distally. Vertex brown, warts slightly paler. Thorax brown, to pale yellowish brown laterally. Legs straw to cream-coloured.

Genitalia. Male. (Fig. 141–144). (Specimen from East White Clay Ck, rt. 926, South Chester Co., Pennsylvania, USA – Holotype). Males distinguished by great elongation, posterad, of all parts of genital capsule, in lateral aspect (Fig. 142, 144); by distal lobes of tergum X, in lateral aspect, almost circular, large; by small, knob-like preanal appendage well anterad of distal lobe of tergum X; by distal lobes of tergum X, in posterior aspect (Fig. 141), really quite small, well separated; and by basal article of clasper sufficiently long to extend dorsad of tergum X.

Genitalia. Female. Unknown.

Biology.— Judging from type locality data it appears that larvae favour at least small streams. Collection date of single known specimen August 3.

Distribution.— Presently known only from Pennsylvania, USA (Map 24).
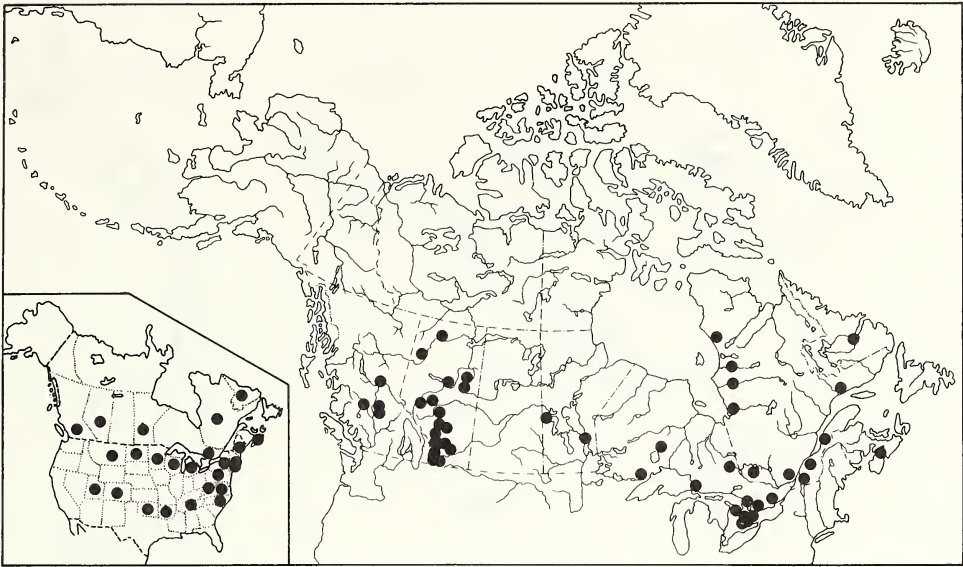
Map 23. Collection localities for *Cheumatopsyche gracilis* (Banks) in Canada, with known distribution in North America by state or province.
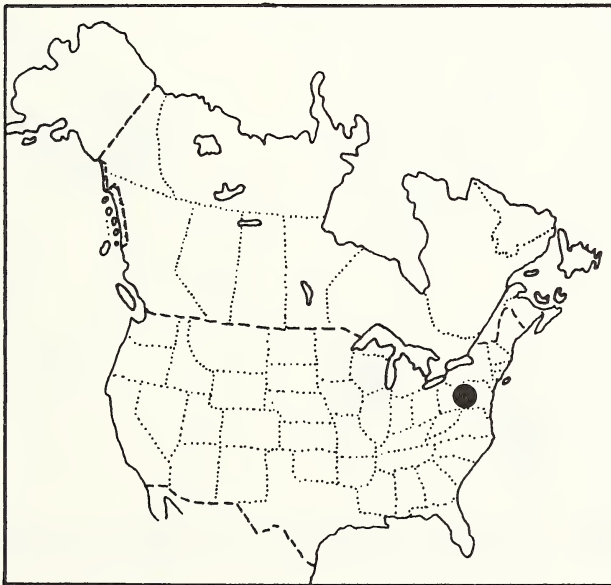

Map 24. Known distribution of *Cheumatopsyche vannotei* Gordon in North America, by state.
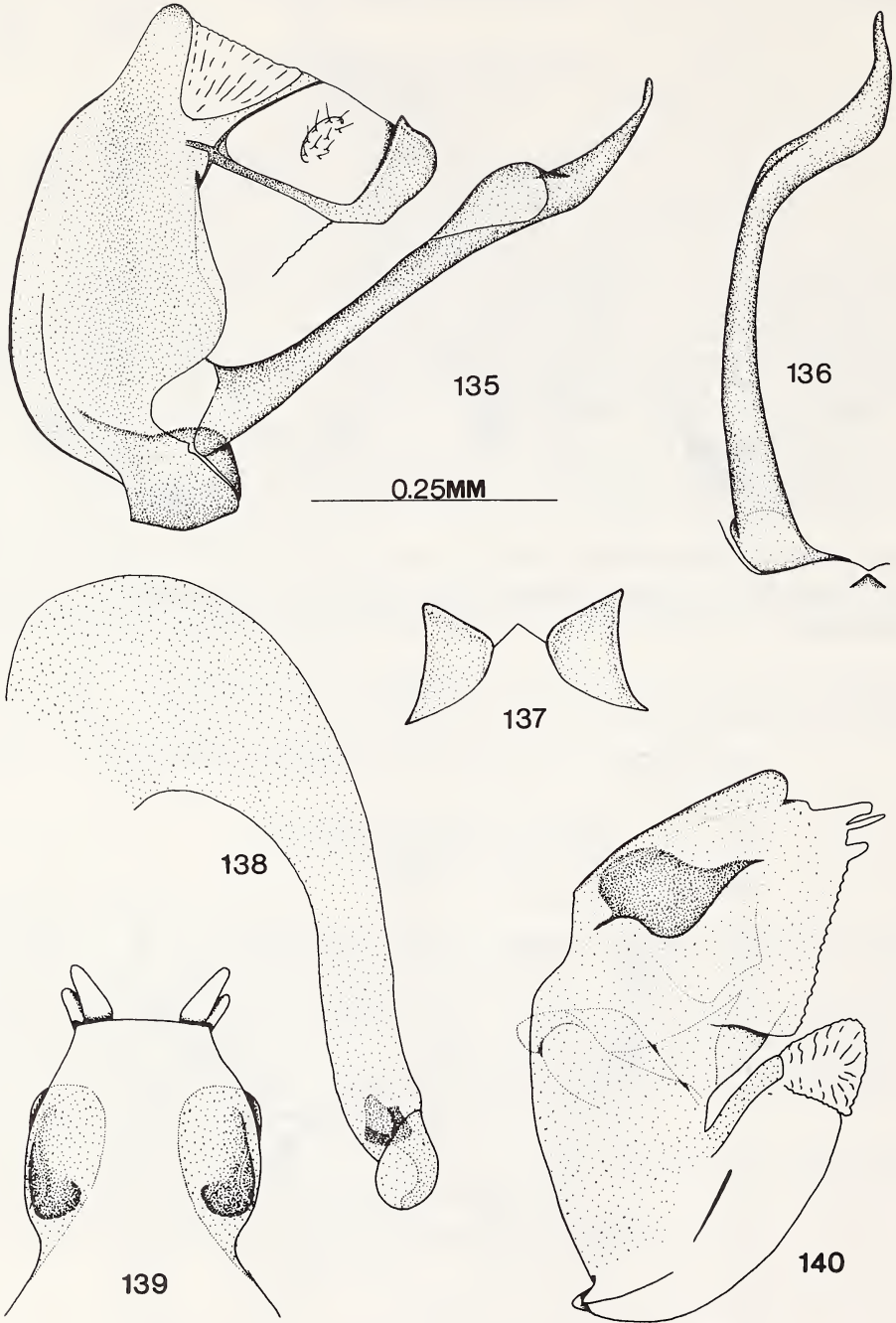
Fig. 135–140, *Cheumatopsyche gracilis* (Banks): 135, genital capsule of male, lateral aspect; 136, left clasper of male, posterior aspect; 137, segment X of male, posterior aspect; 138, aedeagus of male, lateral aspect; 139, genital segments of female, dorsal aspect; 140, genital segments of female, lateral aspect.

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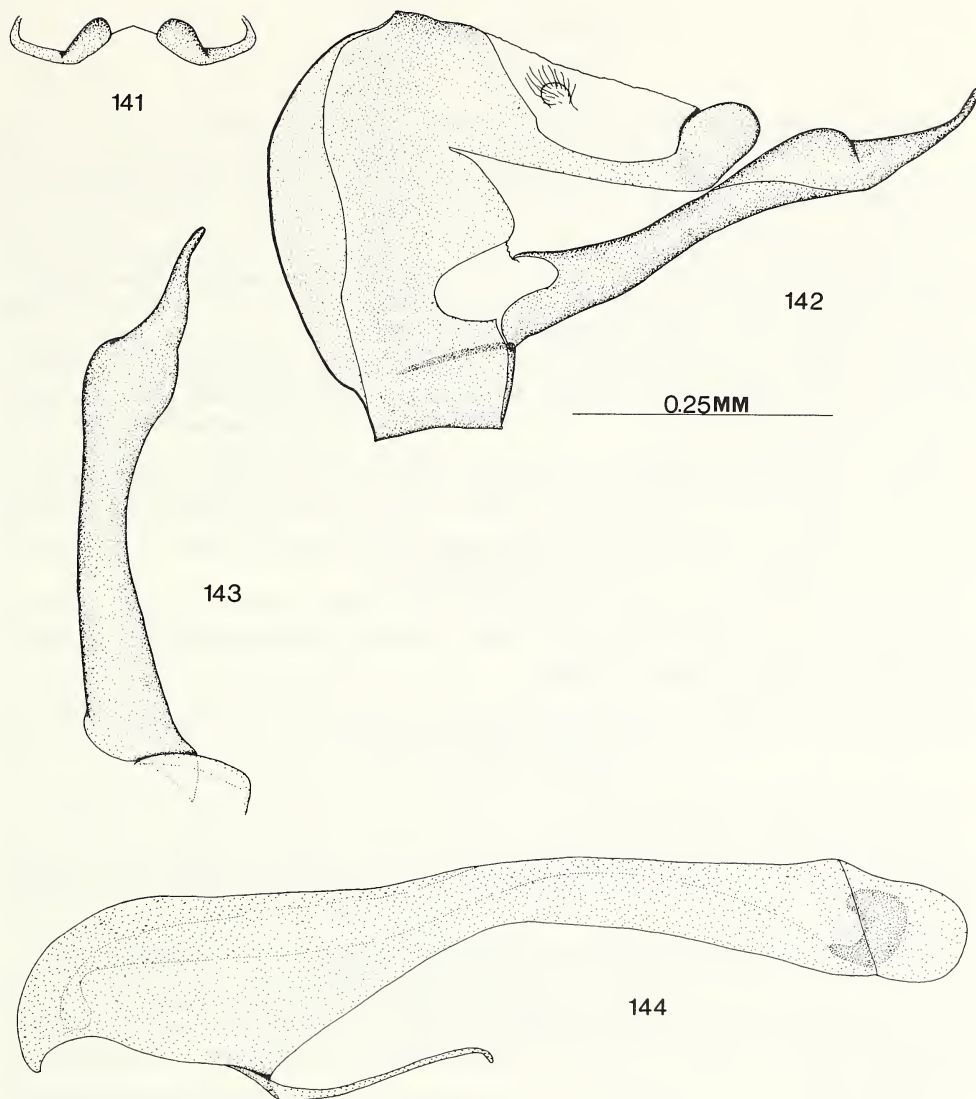
Fig. 141–144, *Cheumatopsyche vannotei* Gordon: 141, segment X of male, posterior aspect; 142, genital capsule of male, lateral aspect; 143, left clasper of male, posterior aspect; 144, aedeagus of male, lateral aspect.

THE *APHANTA* GROUP

Cheumatopsyche oxa Ross
Map 25; Fig. 145–150

Cheumatopsyche oxa Ross, 1938b:155; Denning, 1943:147; Ross, 1944:110; Gordon, 1974:140.

Description.— Male fore-wing length 7.1 mm; grey-brown, with uniform faint irroration. Hind-wing pale grey. Antennae brown, without oblique, dark band on any flagellar annulus. Vertex dark chocolate-brown. Spurs pale brown; lateral member of middle leg pairs, and of hind-leg apical pair, notably shorter than mesal companions. Thorax dark chocolate-brown. Legs pale brown to yellow.

Genitalia. Male. (Fig. 145–148). (Specimen from creek, Hwy 932, S of Whitecourt, Alberta). Males distinguished by dorsal lobes present on segment IX (Fig. 145); by no gap between tergum X and distal lobes; by distal lobes, in posterior aspect (Fig. 148), long, trapezoidal, except distal end slightly expanded, rounded; by distal lobes virtually contiguous; and by distal article of clasper linear, in posterior aspect (Fig. 146), evenly tapered.

Genitalia. Female. (Fig. 149–150). (Specimen from creek, Hwy 932, S of Whitecourt, Alberta). Females distinguished by large clasper receptacle, with inner end curved dorsad, of uniform width, in lateral aspect (Fig. 150); by outer margin of receptacle incised, incision semicircular, directed slightly anterad of dorsal; by inner opening of receptacle evident, of same width as chimney; and by sclerotised strap of vulval scale acute-triangular, with proximal corner connected to base of segment X by thin line.

Biology.— Ross (1944) indicates a preference in larvae for small streams, often spring-fed. This species appears to occur in small, local colonies. Illinois flight dates extend from March to October. Generally, Canadian locality records support Ross. Canadian flight records extend from May 17 to September 2, with diffuse peak in July.

Distribution.— Roughly triangular when mapped, with angles in British Columbia, Québec, and Georgia (Map 25). The Canadian distribution is from central British Columbia to James Bay, and the Eastern Townships of Québec.

Cheumatopsyche aphanta Ross
Map 26; Fig. 151–156

Cheumatopsyche aphanta Ross, 1938b:151; Denning, 1943:151; Ross, 1944:111; Gordon, 1974:140.

Description.— Male fore-wing length 4.64 mm; red-brown. Hind-wing hyaline with red-brown veins. Antennae pale red-brown; basal five flagellar annuli each with oblique, dark band. Vertex deep red-brown. Spurs straw-coloured; lateral member of front and middle leg pairs much shorter than mesal companions. Thorax deep red-brown, to paler laterally. Legs deep straw-coloured.

Genitalia. Male. (Fig. 151–154). (Specimen from Washington Co., Arkansas, USA). Males distinguished by distinct dorsal lobes on segment IX (Fig. 151); by distal lobes of tergum X massive in lateral aspect, rounded, not separated from main body of tergum by gap; by distal article of clasper, in lateral aspect, very much thinner than basal article, with little taper, hooked sharply dorsad at tip; by distal article of clasper, in posterior aspect, with base almost equal in width to basal article, acute-triangular, with slight distal curve; and by distal lobes of tergum X, in posterior aspect (Fig. 153), not very close, spindle-shaped.

Genitalia. Female. (Fig. 155–156). (Specimen from Washington Co., Arkansas, USA). Females distinguished by clasper receptacle outer margin produced ventrad, and postero-dorsad, as large ventral lobe and posterior flange respectively, extended posterad of posterior edge of segment X (Fig. 156); by chimney of receptacle inclined slightly posterad of dorsal, without inner opening visible; and by sclerotised strap of vulval scale expanded evenly, gradually, distad, strap curved, not in contact with base of segment X.

Biology.— Canadian flight season records extend from June 21 to July 20. Ross (1944) records the species as common adjacent to small streams and brooks, especially those which are permanent and spring-fed. Illinois flight season extends from May to late September.

Distribution.— From North Dakota to New York, south to Arkansas in the USA (Map 26). In Canada this species is presently known only from northeastern New Brunswick and the Eastern Townships of Québec.

Cheumatopsyche halima Denning
Map 27; Fig. 157–162

Cheumatopsyche halima Denning, 1948:400; Gordon, 1974:141.

Description.— Male fore-wing length 6.36 mm; uniform grey-brown. Hind-wing tinted pale grey-brown. Antennae pale brown; basal five flagellar annuli each with oblique, darker band. Vertex very dark chocolate, to black-brown. Spurs straw; lateral member of front leg pair much smaller than mesal companion. Thorax very dark chocolate to black-brown, to slightly paler laterally. Legs dark grey-brown.

Genitalia. Male. (Fig. 157–160). (Specimen from St Hippolyte, Québec). Males distinguished by lack of dorsal lobes on segment IX (Fig. 157); by very small, v-shaped notch between tergum X and distal lobes; by distal lobes of tergum X, in posterior aspect (Fig. 159), triangular, close to each other; and by distal article of clasper, in posterior aspect (Fig. 158), distinct from basal article, width sharply reduced at junction of the two – distal article curved dorso-laterad.

Genitalia. Female. (Fig. 161–162). (Specimen from St Hippolyte, Québec). Females distinguished by clasper receptacle, in lateral aspect (Fig. 162), curved dorso-posterad, with inner opening visible; and by outer margin of receptacle developed postero-ventrad as large, rounded lobe which partly overlaps posterior edge of segment X.

Biology.— Massachusetts flight season given by Neves (1979) as June to August. Available Canadian records give a range of June 21 to July 25. Habitat information rare, but larvae are known to inhabit small streams to small rivers.

Distribution.— Known from Arkansas northeastern states of USA (Map 27). In Canada this species is recorded from southern Québec and New Brunswick.

Cheumatopsyche mollala Ross
Map 28; Fig. 163–168

Cheumatopsyche mollala Ross, 1941:81; Ross, 1944:294; Gordon, 1974:142.

Description.— Male fore-wing length 6.47 mm; pale grey-brown, faintly irrorate posterad of Cu1 + 2, and along costal margin. Hind-wing uniform grey. Antennae brown; basal seven flagellar annuli each with oblique, dark band. Vertex deep chocolate-brown, warts paler. Spurs yellowish; lateral member of middle leg apical pair, and hind-leg apical pair, shorter than mesal companions; in female, only laterals of middle leg shorter than mesals. Thorax deep chocolate-brown throughout; paler laterally in female; warts paler. Legs straw-coloured.

Genitalia. Male. (Fig. 163–166). (Specimen from Lobster Ck, 15 miles SW of Alsea, Benton Co., Oregon, USA). Males distinguished by small, distinct dorsal lobes on segment IX (Fig. 163); by tergum X slightly humped dorsad in lateral aspect; by distal lobes of tergum X dorsally acuminate, triangular, without gap between them and main body of tergum X; by distal lobes, in posterior aspect (Fig. 165), triangular – dorsal angle of each acuminate, directed dorso-laterad; and by distal article of clasper, in posterior aspect (Fig. 164), with basal three quarters stout, directed mesad, and distal quarter thin, acuminate, directed dorsad.

Genitalia. Female. (Fig. 167–168). (Specimen from Lobster Ck, 15 miles SW of Alsea, Benton Co., Oregon, USA). Females distinguished by distinctive, bell-shaped clasper receptacle, in lateral aspect (Fig. 168); by inner portion of chimney directed dorsad; and by inner opening of recepta le not visible.

Biology.— The sole Canadian record is from May 26. Anderson (1976) gives a flight season for Oregon from late May to early September, with no definable peak. It is unclear what types of flowing waters the larvae may favour.

Distribution.— Very spotty (Map 28). Known from Oregon, Idaho, California, and Arkansas in United States, and eastern Ontario in Canada.

Cheumatopsyche burksi Ross
Map 29; Fig. 169–175

Cheumatopsyche burksi Ross, 1941:83; Ross, 1944:113; Gordon, 1974:142.

Description.— Male fore-wing length 7.45 mm; grey-brown; faintly, uniformly irrorate. Antennae yellow-brown; basal six flagellar annuli each with oblique, faintly darker band; five in female. Vertex deep red-brown, warts slightly paler. Spurs brown; lateral member of middle and hind-leg pairs noticeably shorter than mesal companions. Thorax deep red-brown, to yellow-brown laterally. Legs yellow-brown to straw.

Genitalia. Male. (Fig. 169–172). (Specimen from Tavares, Lake Co., Florida, USA – Paratype). Males distinguished by distinct dorsal lobes on segment IX (Fig. 169); by small distal lobes of tergum X, in lateral aspect, hardly separable from main body of tergum; by distal article of clasper with wide basal third surmounted by aristate, dorsally curved distal two-thirds, in lateral aspect; by distal article of clasper, in posterior aspect (Fig. 170), much as above, except junction between basal and distal portions more gradual; and by distal lobes of tergum X, in posterior aspect (Fig. 172), well separated, expanded dorsal portion ovoid.

Genitalia. Female. (Fig. 173–175). (Specimen from Tavares, Lake Co., Florida, USA – Allotype). Females distinguished by medium-sized clasper receptacle bell-like, but skewed anterad in lateral aspect (Fig. 174); and by posterior edge of each half of sternite VIII irregular (Fig. 175), with small, triangular process slightly higher than mid-point.

Biology.— The only flight date available is October 2, in Illinois (Ross, 1944). Nothing more known at present.

Distribution.— Presently known only from Illinois to Louisiana and Florida, USA (Map 29).

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Cheumatopsyche enonis Ross
Map 30; Fig. 176–181

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Cheumatopsyche enonis Ross, 1938b:153; Ross, 1944:294; Gordon, 1974:142.
Cheumatopsyche geolca Denning, 1952:21; Gordon, 1974:142.

Description.— Male fore-wing length 4.99 mm; grey, almost hyaline. Hind-wing hyaline. Antennae brown. Vertex dark brown. Spurs yellow; lateral member of middle leg pairs shorter than mesal companions. Thorax dark red-brown, to paler laterally. Legs yellow.

Genitalia. Male. (Fig. 176–179). (Specimen from Dale Ck, Richland, Oregon, USA). Males distinguished by very prominent dorsal lobes of segment IX (Fig. 176); by small, tapered distal lobes of tergum X directed postero-dorsad in lateral aspect; by distal lobes fairly close, trapezoidal in posterior aspect (Fig. 179); and by conical distal article of clasper with meso-ventral spur, in posterior aspect (Fig. 177).

Genitalia. Female. (Fig. 180–181). (Specimen from Dale Ck, Richland, Oregon, USA). Females distinguished by clasper receptacle, in lateral aspect (Fig. 181), located dorso-anterad in segment X; by receptacle directed anterad; by receptacle inner opening not visible in lateral aspect [if such an opening exists – not visible in dorsal aspect either (Fig. 180)]; and by vulval scale apparently without sclerotised strap.

Biology.— Anderson (1976) has no comment on habitats, but locality names suggest that larvae frequent creeks and, at least, smaller rivers. Oregon flight season is given as June to early September.

Distribution.— Recorded from all western cordilleran states of USA, except Washington, California, and Arizona (Map 30).
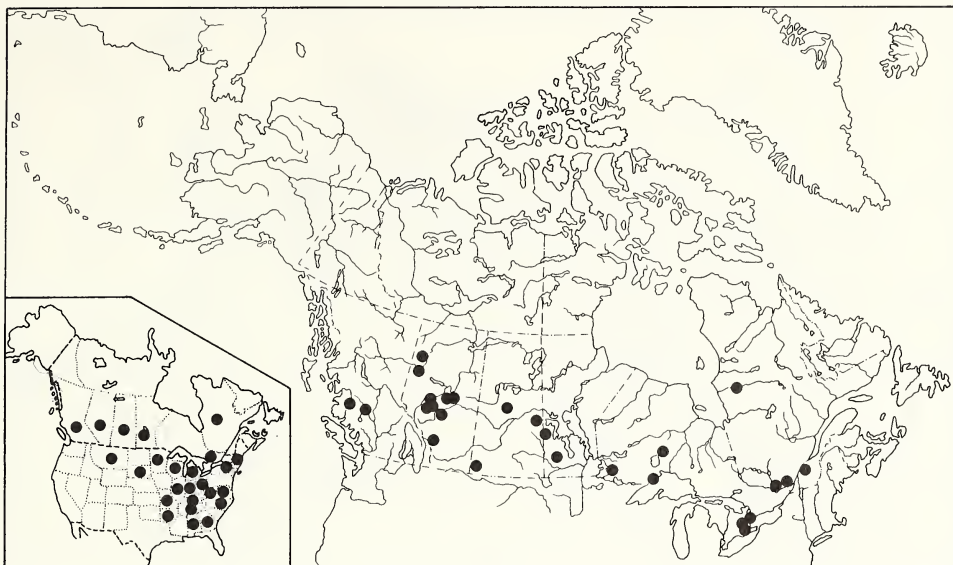
Map 25. Collection localities for *Cheumatopsyche oxa* Ross in Canada, with known distribution in North America by state or province.
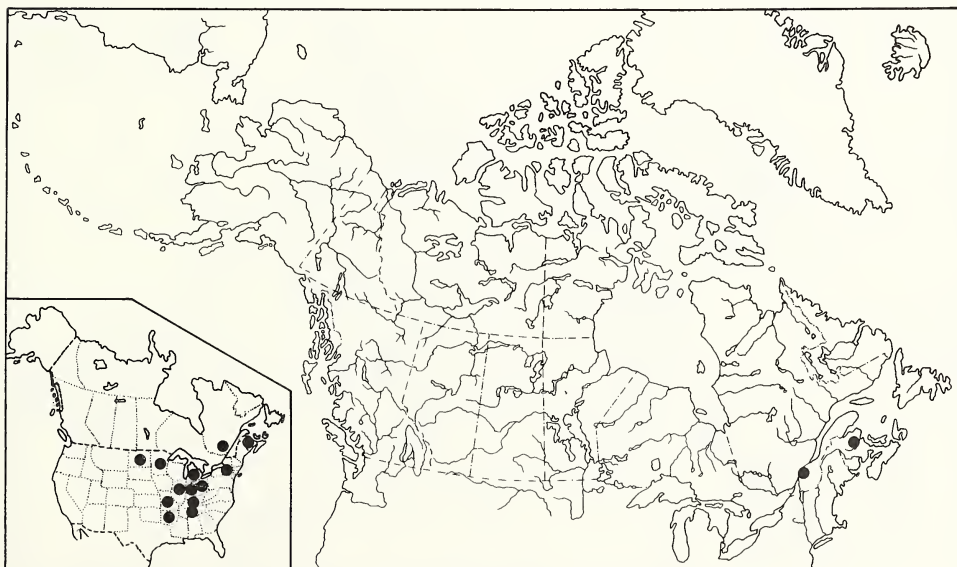
Map 26. Collection localities for *Cheumatopsyche aphanta* Ross in Canada, with known distribution in North America by state or province.

Map 27. Collection localities for *Cheumatopsyche halima* Denning in Canada, with known distribution in North America by state or province.
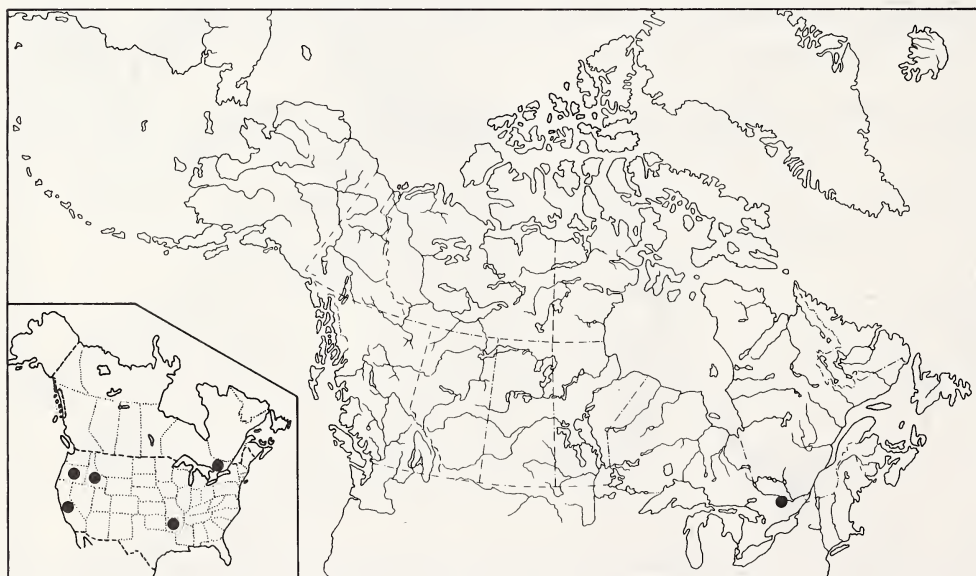
Map 28. Collection localities for *Cheumatopsyche mollala* Ross in Canada, with known distribution in North America by state or province.

Map 29. Known distribution of *Cheumatopsyche burksi* Ross in North America, by state.
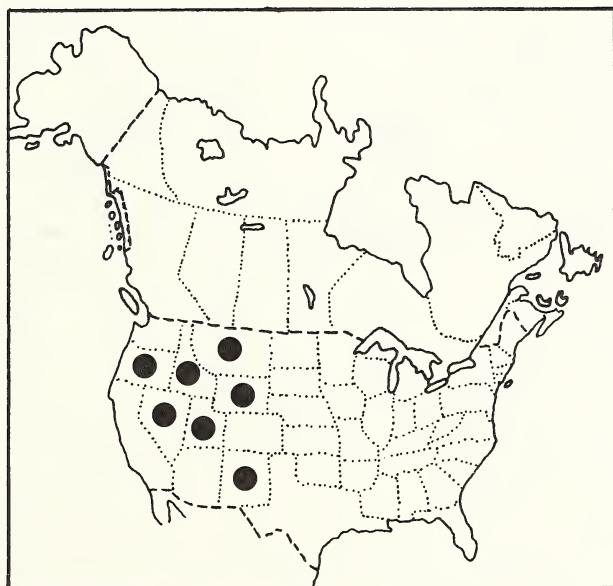
Map 30. Known distribution of *Cheumatopsyche enonis* Ross in North America, by state.
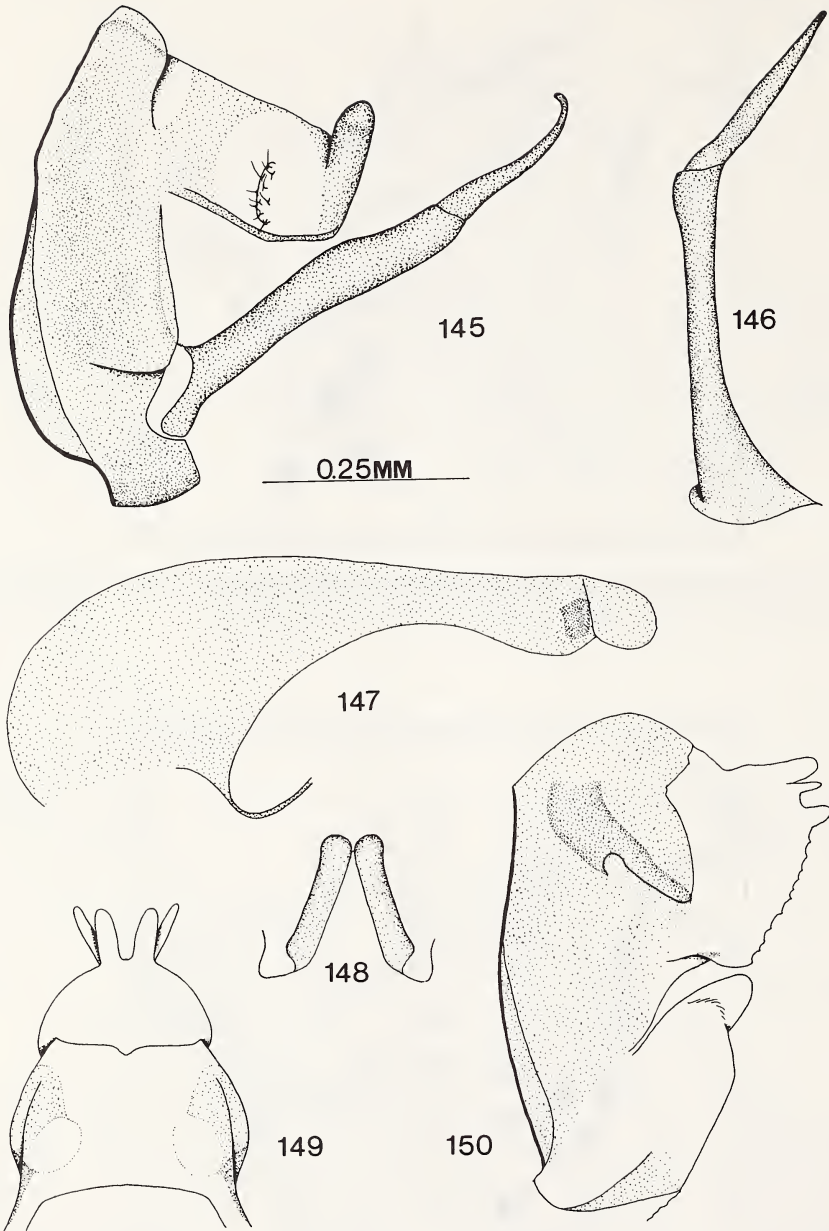
Fig. 145–150, *Cheumatopsyche oxa* Ross: 145, genital capsule of male, lateral aspect; 146, left clasper of male, posterior aspect; 147, aedeagus of male, lateral aspect; 148, segment X of male, posterior aspect; 149, genital segments of female, dorsal aspect; 150, genital segments of female, lateral aspect.
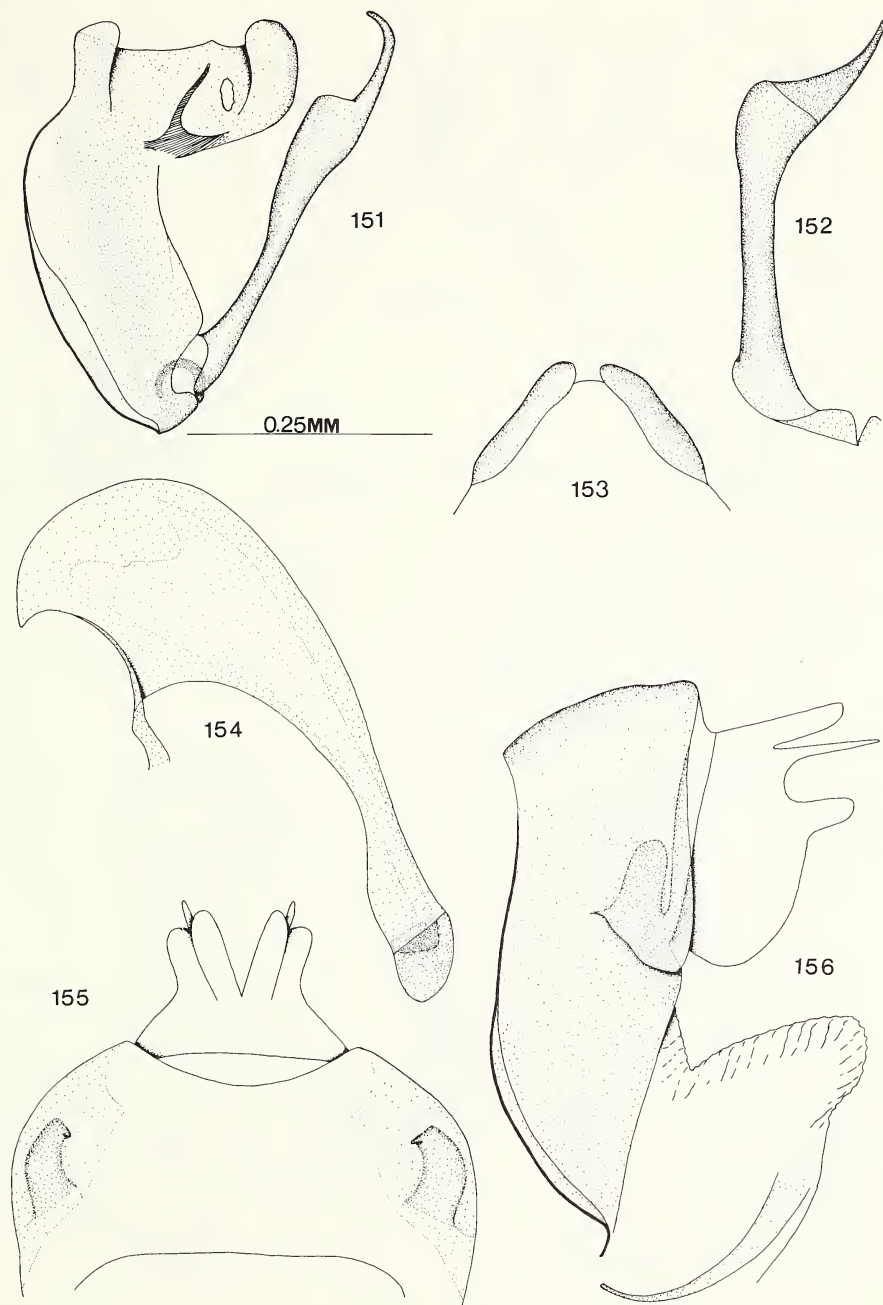
Fig. 151–156, *Cheumatopsyche aphanta* Banks: 151, genital capsule of male, lateral aspect; 152, left clasper of male, posterior aspect; 153, segment X of male, posterior aspect; 154, aedeagus of male, lateral aspect; 155, genital segments of female, dorsal aspect; 156, genital segments of female, lateral aspect.
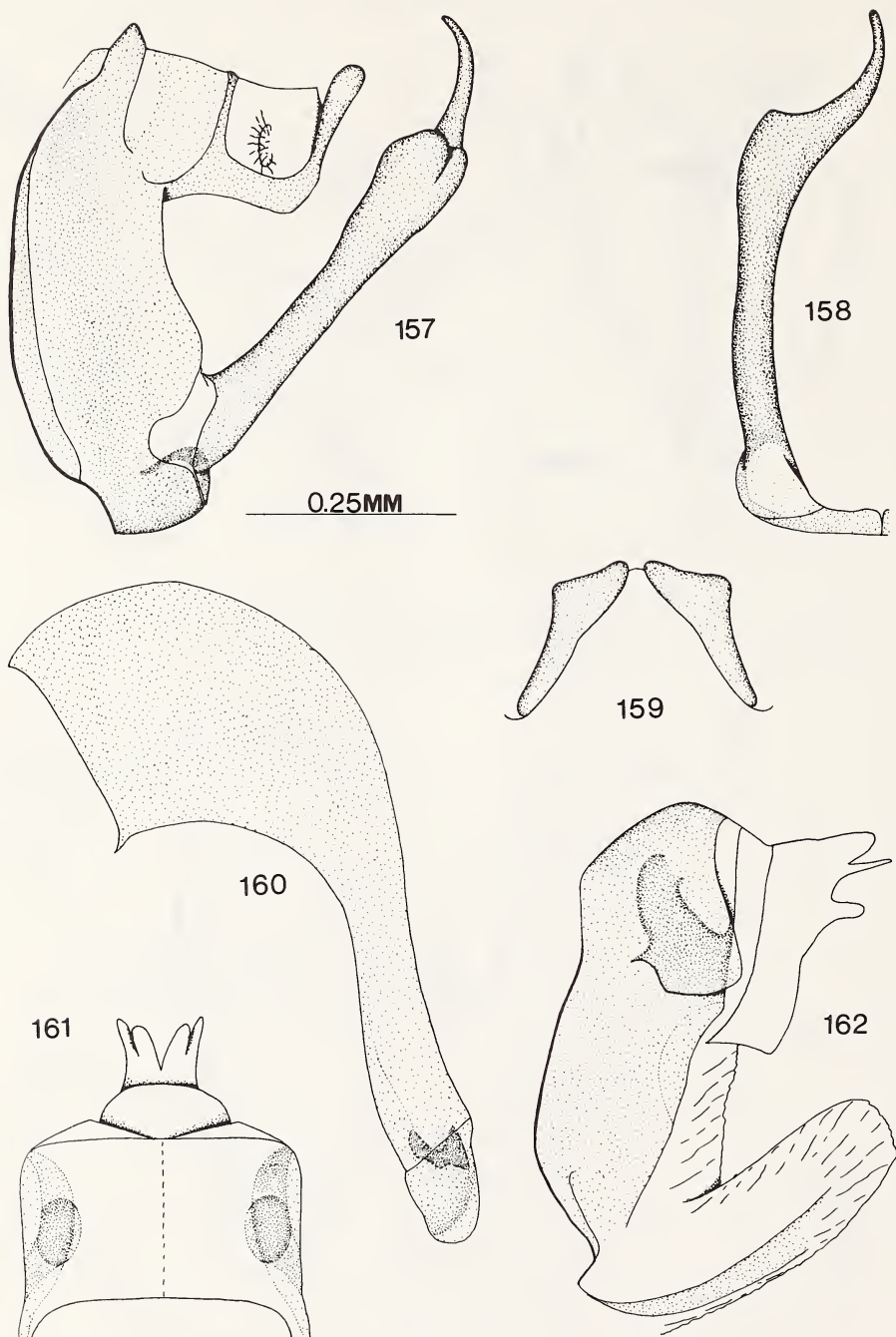
Fig. 157–162, *Cheumatopsyche halima* Denning: 157, genital capsule of male, lateral aspect; 158, left clasper of male, posterior aspect; 159, segment X of male, posterior aspect; 160, aedeagus of male, lateral aspect; 161, genital segments of female, dorsal aspect; 162, genital segments of female, lateral aspect.
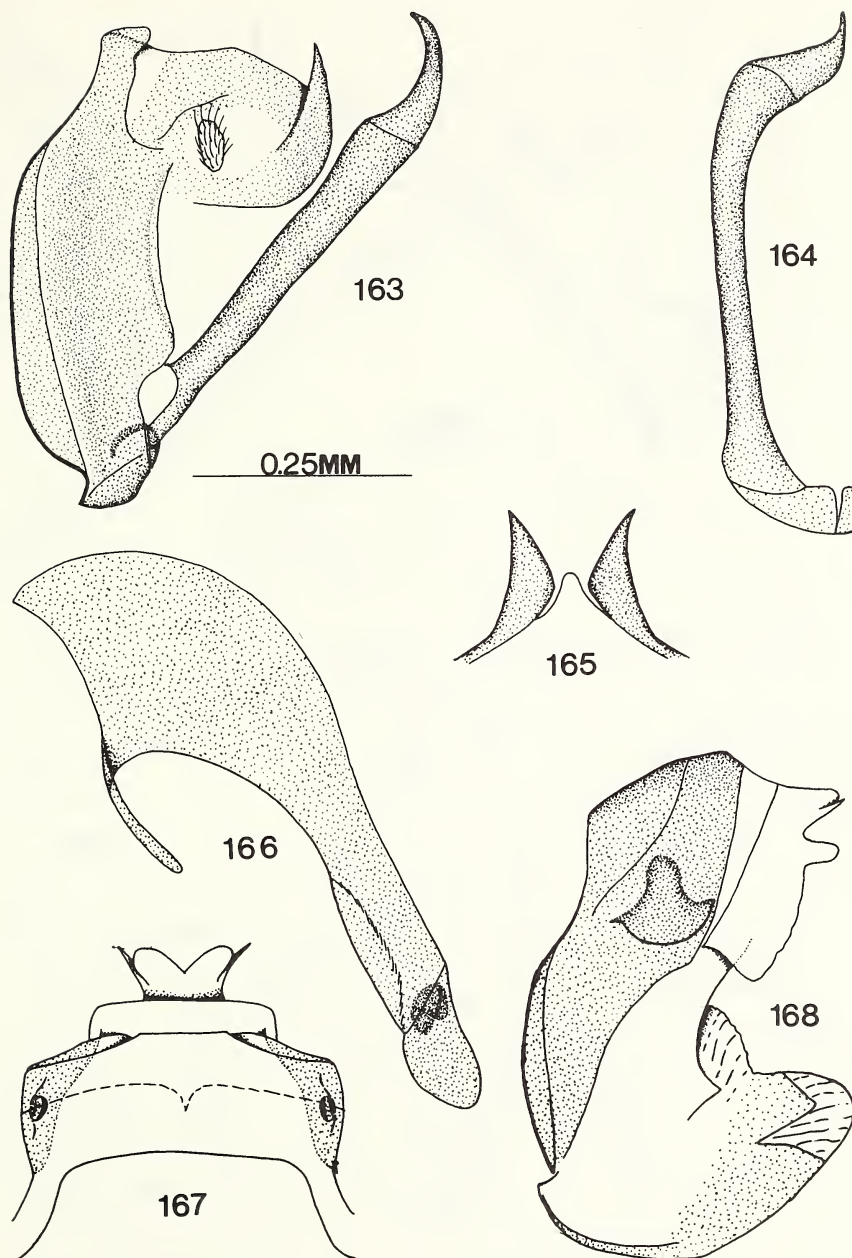
Fig. 163–168, *Cheumatopsyche mollala* Ross: 163, genital capsule of male, lateral aspect; 164, left clasper of male, posterior aspect; 165, segment X of male, posterior aspect; 166, aedeagus of male, lateral aspect; 167, genital segments of female, dorsal aspect; 168, genital segments of female, lateral aspect.
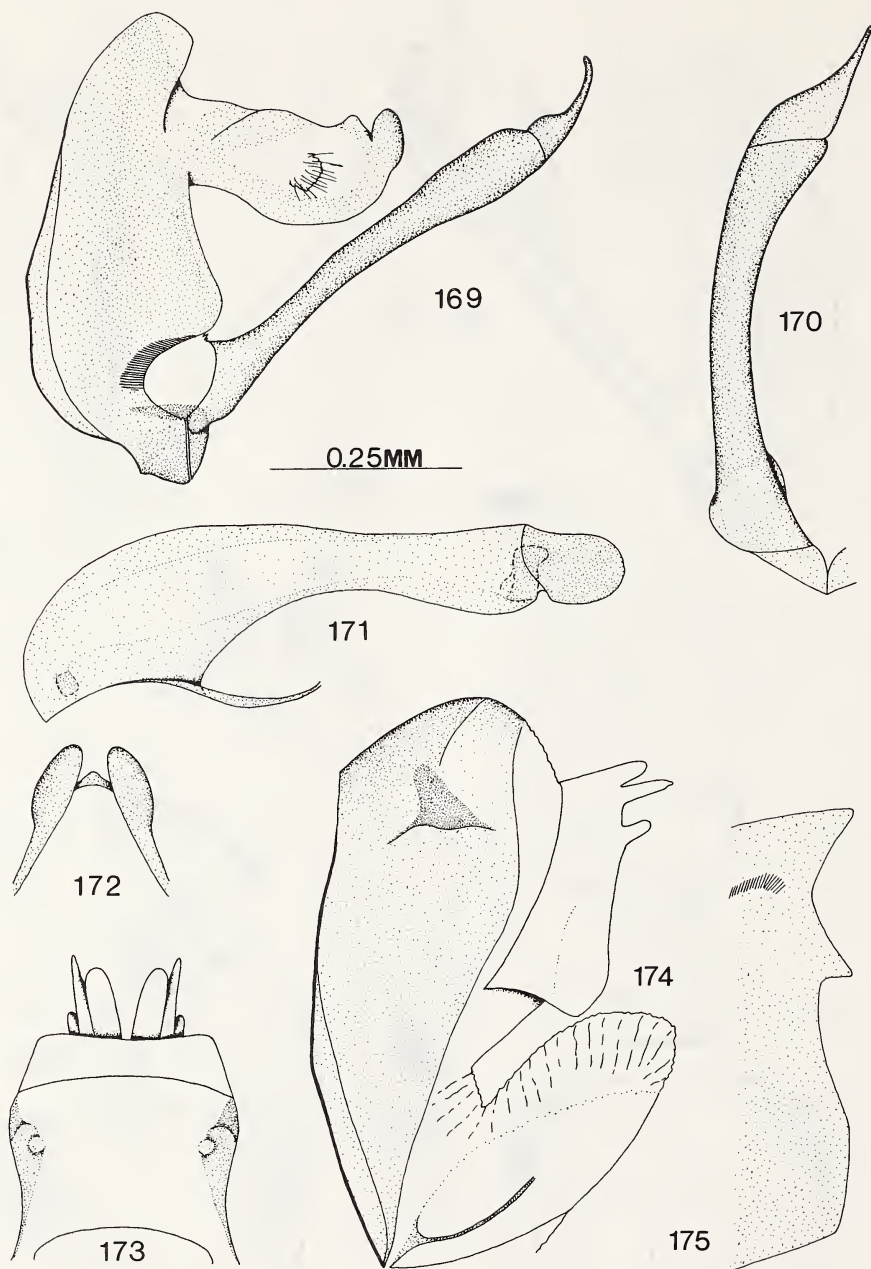
Fig. 169–175, *Cheumatopsyche burksi* Ross: 169, genital capsule of male, lateral aspect; 170, left clasper of male, posterior aspect; 171, aedeagus of male, lateral aspect; 172, segment X of male, posterior aspect; 173, genital segments of female, dorsal aspect; 174, genital segments of female, lateral aspect; 175, left half of sternite VIII of female, lateral aspect.
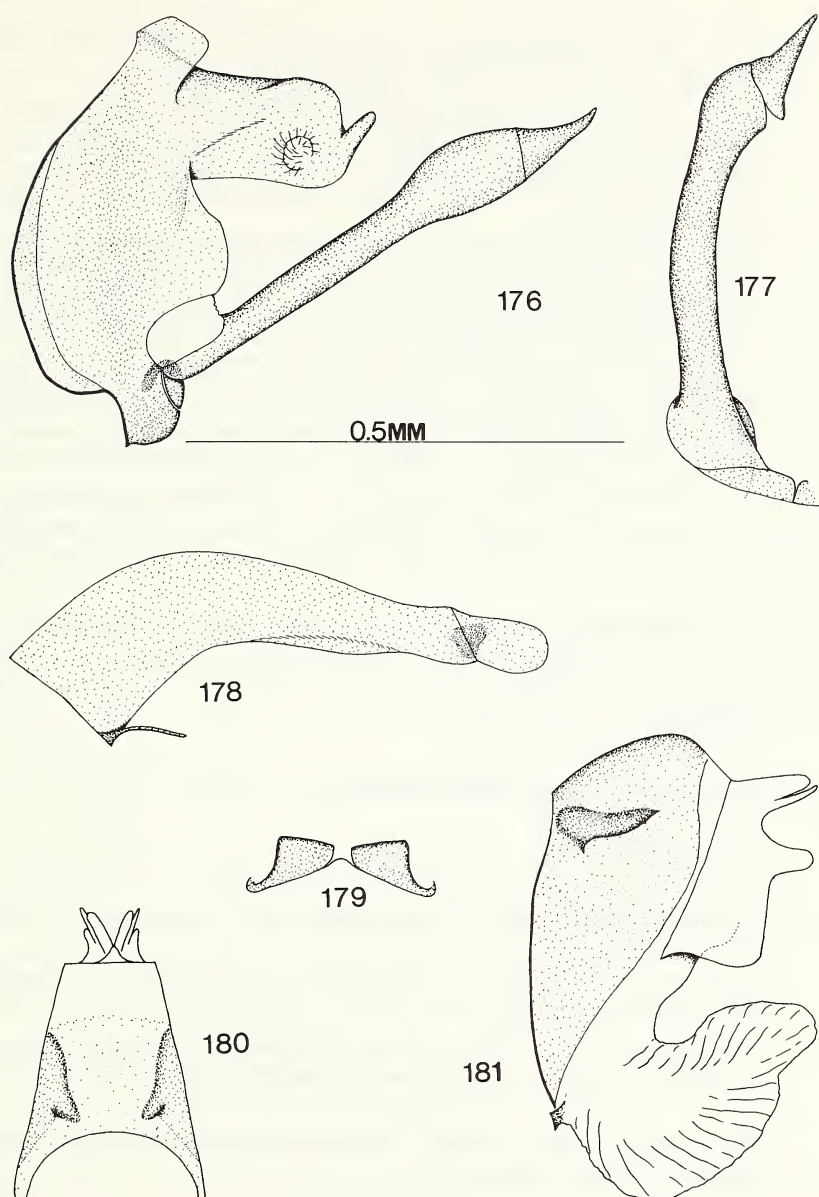
Fig. 176–181, *Cheumatopsyche enonis* Ross: 176, genital capsule of male, lateral aspect; 177, left clasper of male, posterior aspect; 178, aedeagus of male, lateral aspect; 179, segment X of male, posterior aspect; 180, genital segments of female, dorsal aspect; 181, genital segments of female, lateral aspect.

Genus *Hydropsyche* Pictet
Map 31–71; Fig. 5, 182–462

Hydropsyche Pictet, 1834:199; McLachlan, 1878:355, 357; Betten, 1934:183; Milne, 1936:68; Denning, 1943:108; Ross, 1944:86; Ross & Unzicker, 1977:310; Wiggins, 1977:106; Schmid, 1980:58.
Symphitopsyche Ulmer, 1907:32; Ross & Unzicker, 1977:304; Schuster & Etnier, 1978:30.

*Description.*— Tarsal claws similar on all three pairs of legs; twisted asymmetrically; overhung by heavy, black hairs. Spur formula 2,4,4. Male sternite V lobe with aperture of large internal gland of two cavities; lobe more or less developed depending on species; gland small, spherical, in female, with only one slightly developed lobe. Cross-veins M3+4-Cu1 and Cu1-Cu2 of fore-wing clearly separated (Fig. 5a). Hind-wing (Fig. 5b) fI petiolate; median cell closed; stems of M and Cu1 parallel, very close.

Genitalia. Male. (Fig. 182–186, 304–308, 332–336, *etc.*). Segment IX with postero-lateral margin developed posterad (Fig. 189), with long setae (not shown). Segment X simple or complex, massive with specifically characteristic lobes (Fig. 182, 183). Claspers (inferior appendages) with stout, conical distal article. Aedeagus curved ventrad basally (Fig. 185, 307, 335); bilobed distally, simple or complex; comprised of sclerotised phallotheca with tip cleft in species groups 1 (Fig. 186) and 2 (Fig. 308). No distal cleft in species group 3, but short, erectile endotheca comprised of lobes of varied complexity (Fig. 335, 336); these lobes variously armed with specifically distinct spines and teeth.

Genitalia. Female. (Fig. 187–188, 309–310, 337–338, *etc.*). Tergite VIII notched on mid-line, with slightly recurved lateral angles in some species. Sternite VIII divided apically to two lobes. Segment X with postero-lateral margin produced as blunt, setate lobe (Fig. 187); with clasper receptacle or lateral depression on dorso-lateral face of segment.

Biology.— Larvae of *Hydropsyche* spp. inhabit a wide range of flowing waters, from largest rivers to spring-fed streamlets, with specific restriction to some lesser range of types. Larvae of *H. alternans* (Walker) and *H. confusa* (Walker) have also been reported from wave-washed shores of larger lakes. Larvae ingest algae, detritus, and animal matter in seasonally determined proportions.

Hydropsyche, the largest genus of the family, is found in all regions but the Neotropical and Antarctica. Wiggins (1977) estimates that about 70 species are now known from North America. Forty-two of these are presented here, most of which are recorded only from east of the western Cordillera.

Key to known or potential species of *Hydropsyche* Pictet of Canada

5b   Distal article of clasper, in posterior aspect, not curved mesad; narrowed
        distally (Fig. 320, 327) 6
6a (5b) Distal article of clasper, in lateral aspect, smoothly tapered distad, with
        rounded tip turned dorsad (Fig. 325) . . . . *H. depravata* Hagen, p. 119
6b   Distal article of clasper, in lateral aspect, irregularly tapered distad, with
        acuminate tip turned slightly dorsad (Fig. 318) . . . . *H. cuanis* Ross, p. 119
7a (3b) Cleft in aedeagus tip, in dorsal aspect, simple, v-shaped, without notches or
        widenings part-way along sides; cleft long or short, wide or narrow (Fig.
        192, 197, 203, 217, 224, 231, 245, 252) 12
7b   Cleft in aedeagus tip not simple v-shape; variously modified from v-shape
        (Fig. 186, 210, 238, 280, 294) 8
8a (7b) Distal article of clasper with tip curved dorsad in lateral aspect (Fig. 206,
        276, 290) 9
8b   Distal article of clasper with tip not curved dorsad in lateral aspect (Fig.
        182, 234) 11
9a (8a) Distal article of clasper, in posterior aspect, blunt (Fig. 292). Gap between
        distal lobes of segment X, in dorsal aspect, wide, approximately v-shaped
        (Fig. 291) . . . . *H. valanis* Ross, p. 90
9b   Distal article of clasper, in posterior aspect, with disto-lateral process (Fig.
        208, 278) 10
10a (9b) Cleft in aedeagus tip wide in dorsal aspect (Fig. 210) . . . .
        . . . . *H. bidens* Ross, p. 84
10b   Cleft in aedeagus tip very narrow, with slight widening at inner end (Fig.
        280) . . . . *H. scalaris* Hagen, p. 89
11a (8b) Distal lobes of segment X, in lateral aspect (Fig. 182), directed
        postero-dorsad, long, narrow . . . . *H. aerata* Ross, p 83
11b   Distal lobes of segment X directed posterad, short, triangular (Fig. 234) . .
        . . . . *H. hageni* Banks, p. 86
12a (7a) Distal article of clasper, in lateral aspect, with tip transversely truncate to
        greater or lesser degree (Fig. 220, 241, 262, 297) 13
12b   Distal article of clasper, in lateral aspect, with disto-ventral corner of tip
        produced dorsad, or entire tip curved dorsad (Fig. 189, 194, 199, 213, 227,
        248, 255, 269, 283) 16
13a (12a) Distal lobes of segment X, in dorsal aspect, separated by broad, flat,
        v-shaped notch (Fig. 242, 263) 14
13b   Distal lobes of segment X, in dorsal aspect, separated by narrow, deep, v-
        or u-shaped notch (Fig. 221, 297) 15
14a (13a) Distal article of clasper, in lateral aspect, massive, rounded, widened distad
        (Fig. 241) . . . . *H. occidentalis* Banks, p. 87
14b   Distal article of clasper, in lateral aspect, small, trapezoidal, with slight
        projection of disto-ventral corner (Fig. 262) . . . . . . *H. placoda* Ross, p. 88
15a (13b) Segment X with blade-like process on each lateral surface directed dorsad
        (Fig. 220) . . . . *H. dicantha* Ross, p. 85
15b   No such process on segment X (Fig. 297) . . . . . . *H. venularis* Banks, p. 90
16a (12b) Distal lobes of segment X, in dorsal aspect, separated by v-shaped notch
        (wide or narrow) (Fig. 190, 195, 200, 249) 17

29a (28b) Distal article of clasper, in lateral aspect, triangular (Fig. 374). . . . .
. . . . *H. bronta* Ross, p. 138
29b   Distal article of clasper, in lateral aspect, rather like clenched hand with
index finger pointing (Fig. 381) . . . . *H. cheilonis* Ross, p. 138
30a (25b) Ventro-lateral lobe of aedeagus with origin at extreme distal end of
aedeagus (Fig. 342, 349). 31
30b   Ventro-lateral lobe of aedeagus with origin ventrad of endotheca (Fig. 335, 353) . . .
. . 32
31a   Ventro-lateral lobe of aedeagus without distal cluster of spines (Fig.
342) . . . . *H. piatrix* Ross, p. 126
31b   Ventro-lateral lobe of aedeagus with distal cluster of spines (Fig. 349). . . .
. . . . *H. vexa* Ross, p. 127
32a (30b) Distal lobe of segment X, in lateral aspect (Fig. 332), massive, blunt; in
dorsal aspect (Fig. 333) almost linear . . . . *H. amblis* Ross, p. 126
32b   Distal lobe of segment X, in lateral aspect (Fig. 353), thin, angled; in
dorsal aspect (Fig. 354), distal ends of lobe curved mesad, gap between
partly enclosed . . . . *H. walkeri* Betten & Mosely, p. 127
33a (24b) Dorsal lobes membranous only, without teeth or spines (Fig. 452,
459) . . . . subgroup F p. 160 34
33b   Dorsal lobes membranous, with teeth and/or spines (Fig. 363, 412, 438) 35
34a (33a) Distal article of clasper, in lateral aspect (Fig. 449), long, tapered from
wide base to slender tip . . . . *H. oslari* Ross, p. 160
34b   Distal article of clasper, in lateral aspect (Fig. 456), shorter, blunt, not
tapered . . . . *H. ventura* Ross, p. 160
35a (33b) Dorsal lobe of aedeagus with one large tooth, and separate cluster of spines
(Fig. 439, 445). . . . . subgroup E p. 156 36
35b   Dorsal lobe with single tooth only (Fig. 363, 412). 37
36a (35a) Tooth at distal extremity of lobe; spine cluster laterally (Fig. 438, 439) . . .
. . . . *H. riola* Denning, p. 156
36b   Spine cluster at distal extremity; tooth laterally (Fig. 445, 446) . . . .
. . . . *H. sparna* Ross, p. 156
37a (35b) Distal tooth of dorsal lobe of aedeagus curved dorsad (Fig. 412, 419, 426,
433) . . . . subgroup D p. 148 38
37b   Distal tooth curved or directed ventrad (Fig. 363, 370) . . . .
. . . . subgroup B p. 134 41
38a (37a) Distal lobes of segment X, in lateral aspect, curved ventrad (Fig. 409, 416). 39
38b   Distal lobes straight, directed postero-dorsad (Fig. 423, 430) 40
39a (38a) Distal lobes of segment X, in dorsal aspect (Fig. 410), linear. . . . .
. . . . *H. alternans* (Walker), p. 148
39b   Distal lobes, in dorsal aspect (Fig. 416), curved postero-mesad . . . .
. . . . *H. centra* Ross, p. 148
. . . . *H. aenigma* Schefter, Wiggins, & Unzicker, p. 148
40a (38b) Distal lobes of segment X, in dorsal aspect (Fig. 424), directed
postero-laterad. . . . . *H. cockerelli* Banks, p. 149
40b   Distal lobes curved slightly postero-mesad (Fig. 431). . . . .
. . . . *H. jewetti* Denning, p. 149

. . . . *H. confusa* (Walker), p. 118

51b   Outer margin with acuminate secondary incision on margn (Fig. 309). Dorsum of segment X narrow . . . . *H. betteni* Ross, p. 118

52a (43b) Dorsum of segment X, in lateral aspect, with (Fig. 211, 239, 253, 288, 295) or without (Fig. 232) slight indentation; thin, black line with origin at indentation, extended across dorso-lateral area of segment X toward clasper receptacle 53

52b   Without either indentation or line (Fig. 204, 225, 302) 57

53a (51a) Clasper receptacle, in dorsal aspect, simple, domed depression, without ventral portion overlapped by dorsal portion (Fig. 212, 233, 254) 54

53b   Clasper receptacle with overlap of ventral portion by dorsal, secondary invagination of segment X wall (Fig. 240, 289, 296) 55

54a (53a) Sclerotised strap of vulval scale simple, thin line (Fig. 232) . . . . *H. frisoni* Ross, p. 85

54b   Sclerotised strap large, width irregular (Fig. 253) . . . . *H. orris* Ross, p. 87

55a (53b) Outer margin of clasper receptacle, in lateral aspect, with distinct, acuminate tooth, closer to posterior end of margin (Fig. 295) . . . . *H. valanis* Ross, p. 90.

55b   Outer margin of clasper receptacle simple (Fig. 239, 288) 56

56a (55b) Vulval scale with angular secondary sclerotised strap (Fig. 239) . . . . *H. hageni* Banks, p. 86

56b   Vulval scale without secondary strap (Fig. 288) . . *H. simulans* Ross, p. 90

57a (52b) Vulval scale with angular secondary sclerotised strap (Fig. 302) . . . . *H. venularis* Banks, p. 90

57b   Vulval scale without secondary strap 58

58a (57b) Clasper receptacle, in lateral aspect (Fig. 225), transverse declivity, with extremities directed ventrad; posterior extremity with slight invagination . . . . *H. dicantha* Ross, p. 85

58b   Clasper receptacle with shallow dorsal pouch, continued ventro-posterad by declivity (Fig. 204) . . . . *H. arinale* Ross, p. 84

59a (42b) Floor of clasper receptacle aperture, in lateral aspect, without grooves or folds (Fig. 267, 281, 337, 407, 428, 461) 60

59b   Floor of clasper receptacle aperture with grooves or folds (Fig. 187, 344, 365, 372, 379, 414, 421, 454) 65

60a (59a) Clasper receptacle, in lateral aspect, associated with declivity (Fig. 267, 281) 61

60b   Clasper receptacle not associated with declivity (Fig. 337, 407, 428, 461) 62

61a (60a) Clasper receptacle outer opening integrated with declivity (Fig. 281) . . . . *H. scalaris* Hagen, p. 89

61b   Clasper receptacle posterad of declivity; receptacle single, circular hole (Fig. 267) . . . . *H. placoda* Ross, p. 88

62a (60b) Sclerotised strap of vulval scale small; irregularly narrow, or just thin, dark line (Fig. 337, 407) 63

62b   Sclerotised strap of vulval scale large, long, widest at two-thirds of length (Fig. 428, 461) 64

63a (62a) Clasper receptacle minute, in lateral aspect; directed dorsad, not associated

with thin, dark line down lateral face of segment X (Fig. 407) . . . .
. . . . *H. tana* Ross, p. 140

63b   Clasper receptacle small, directed anterad; thin, dark line extended across
          mouth of receptacle (Fig. 337) . . . . *H. amblis* Ross, p. 126

64a (62b) Clasper receptacle small, directed dorso-anterad, located low down on
          lateral face of segment X (Fig. 428) . . . . *H. cockerelli* Banks, p. 149

64b   Clasper receptacle large, oriented vertically, directed anterad, located more
          dorsally on segment X (Fig. 461) . . . . *H. ventura* Ross, p. 160

65a (59b) Inner opening of clasper receptacle not visible in lateral aspect (Fig. 187,
          421, 454) 66

65b   Inner opening visible in lateral aspect (Fig. 344, 414) 68

66a (65a) Clasper receptacle, in lateral aspect, with single groove on floor of aperture
          (Fig. 187). . . . . *H. aerata* Ross, p. 83

66b   Clasper receptacle with two grooves (Fig. 421, 454). 67

67a (66b) Clasper receptacle directed dorsad in lateral aspect (Fig. 421), posterad in
          dorsal aspect (Fig. 422) . . . . *H. centra* Ross, p. 148

67b   Clasper receptacle directed dorso-anterad in lateral aspect (Fig. 454),
          mesad in dorsal aspect (Fig. 455). . . . . *H. oslari* Ross, p. 160

68a (65b) Clasper receptacle outer margin, in lateral aspect, with both ends on same
          level (Fig. 344, 414) 69

68b   Clasper receptacle with outer margin anterior end lower than posterior end
          (Fig. 372, 379, 393). 70

68c   Clasper receptacle outer margin with anterior end higher than posterior
          end (Fig. 351, 365, 400, 440, 447) 73

69a (68a) Clasper receptacle, in lateral aspect, curved dorso-posterad (Fig. 344) . . . .
          . . . . *H. piatrix* Ross, p. 126

69b   Clasper receptacle, in lateral aspect, directed dorso-anterad (Fig. 414) . . .
          . . . . *H. alternans* (Walker), p. 148

70a (68b) Clasper receptacle, in dorsal aspect, curved meso-posterad (Fig. 373, 387) 71

70b   Clasper receptacle directed mesad in dorsal aspect (Fig. 380, 394) 72

71a (70a) Outer margin of clasper receptacle, in lateral aspect, angularly incised
          (Fig. 372). . . . . *H. bifida* Banks, p. 134

71b   Outer margin slightly sinuate, not incised (Fig. 386) . . . .
          . . . . *H. cheilonis* Ross, p. 138

72a (70b) Outer margin of clasper receptacle, in lateral aspect, continued to either
          side by thin, dark line (Fig. 379) . . . . *H. bronta* Ross, p. 138

72b   No such thin, dark line present (Fig. 393) . . . . . . *H. morosa* Hagen, p. 139

73a (68c) Cerci, dorsal and ventral lobes of segment XI, in dorsal aspect, visible (Fig.
          366, 401, 448) 74

73b   At most, only dorsal lobes, cerci visible in dorsal aspect (Fig. 352, 441) 76

74a (73a) Anterior end of clasper receptacle outer margin continued ventrad as thin,
          dark line (Fig. 400) . . . . *H. slossonae* Banks, p. 139

74b   No such continuation of clasper receptacle outer margin (Fig. 365, 447) 75

75a (74b) Posterior end of clasper receptacle outer margin, and outer ends of grooves
          on floor of receptacle, approximately in line (Fig. 365) . . . .
          . . . . *H. alhedra* Ross, p. 134

75b   These points not in line (Fig. 447) .... *H. sparna* Ross, p. 156

76a (73b) Lobe of postero-lateral margin of segment X small, triangular (Fig. 351)

.... *H. vexa* Ross, p. 127

76b   Lobe long, hemi-elliptical (Fig. 440) .... *H. riola* Denning, p. 156

SPECIES GROUP 1

This group is characterised by aedeagus sclerotised throughout, without membranous lobes, with distal tip wedge-shaped in lateral aspect (*e.g.,* Fig. 185).

Hydropsyche aerata Ross
Map 31; Fig. 182–188

Hydropsyche aerata Ross, 1938b:144; Ross, 1944:101; Schuster & Etnier, 1978:77.

Description.— Male fore-wing length 7.02 mm; light brown; faintly, coarsely irrorate posterad of Cu1+2. Hind-wing hyaline. Antennae red-brown, no markings in male; allotype female with at least three basal flagellar annuli with dark, oblique bands (remainder of antennae missing). Vertex deep red-brown; narrow in male – eyes very large relative to head; normal in allotype female. Spurs yellow; lateral member of all pairs notably shorter than mesal companions. Thorax uniformly deep red-brown. Legs yellow.

Genitalia. Male. (Fig. 182-186). (Specimen from Aroma Park, Kankakee R., Illinois, USA). Males distinguished by distal lobes of segment X approximately rectangular in lateral aspect (Fig. 182), directed postero-dorsad; by distal article of clasper, in lateral aspect, relatively little tapered, without distal hook; by distal cleft of aedeagus, in dorsal aspect (Fig. 186), not v-shaped, widened laterad at mid-point; and by distal article of clasper, in posterior aspect (Fig. 184), parallel-sided, truncate distally.

Genitalia. Female. (Fig. 187, 188). (Specimen from Oakwood, Illinois, USA – Allotype). Females distinguished by clasper receptacle, in lateral aspect (Fig. 187), simple, broad, rounded invagination with inner opening not visible, with one groove on receptacle floor; by receptacle, in dorsal aspect (Fig. 188), with ventral portion overlapped by dorsal portion; and by sclerotised strap of vulval scale proximally acuminate, evenly and considerably widened distally.

Biology.— Poorly known. Ross gives flight season as May to late August. Apparently a species of large rivers with rapids and gravel bottoms.

Distribution.— Not yet known from Canada. In the USA the species is presently only recorded from Illinois, Indiana, and Michigan (Map 31).

Hydropsyche alvata Denning
Map 32; Fig. 189–193

Hydropsyche alvata Denning, 1949:40; Schuster & Etnier, 1978:125; Flint, Voshell, & Parker, 1979:842.

Description.— Male fore-wing length 8.38 mm; pale red-brown, veins darker, faintly irrorate about Cu1+2/RS/M and distal edge. Hind-wing faintly tinted warm red-brown. Antennae pale red-brown; basal 7 or 8 flagellar annuli each with oblique, dark band. Vertex dark red-brown. Spurs straw-coloured; lateral member of fore- and middle leg pairs much shorter than mesal companions. Thorax dark red-brown, to paler laterally. Legs straw-coloured.

Genitalia. Male. (Fig. 189–193). (Specimen from Madison Co., Arkansas, USA). Males distinguished by distal lobes of segment X blunt, triangular in lateral aspect (Fig. 189), short, rounded, separated by u-shaped notch in dorsal aspect (Fig. 190); by distal cleft of aedeagus very narrowly v-shaped in dorsal aspect (Fig. 192); and by distal article of clasper, in lateral aspect (Fig. 189), long, curved slightly dorsad, of even width except for distal taper to upturned tooth.

Genitalia. Female. Unknown.

Biology.— Virtually nothing known. Denning's (1949) original description provides a range of flight dates from March 3 to July 18.

Distribution.— Not yet recorded from Canada. In the USA the species is known from Arkansas to Michigan and Virginia (Map 32).

Hydropsyche arinale Ross
Map 33; Fig. 199–205

Hydropsyche arinale Ross, 1938b:143; Ross, 1944:104; Schuster & Etnier, 1978:86.

Description.— Male fore-wing length 6.32 mm; pale red-brown, with banded pattern in area of anal lobe, with distinct darker bar mid-way along anal edge; faintly irrorate along R1. Hind-wing tinted warm red-brown. Antennae yellow-brown; basal seven flagellar annuli each with oblique, dark band. Vertex pale red-brown. Spurs yellow-brown; lateral member of fore- and middle leg pairs shorter than mesal companions. Thorax deep red-brown, to paler laterally. Legs pale red-brown.

Genitalia. Male. (Fig. 199–203). (Specimen from Washington Co., Arkansas, USA). Males distinguished by distal lobes of segment X, in lateral aspect (Fig. 199), short, broad, rounded, separated, in dorsal aspect (Fig. 200), by shallow, wide, v-shaped notch; by distal article of clasper, in lateral aspect, unevenly tapered to dorsally upturned distal hook; and by distal cleft of aedeagus v-shaped in dorsal aspect, with ventral area not notched (Fig. 203).

Genitalia. Female. (Fig. 204–205). (Specimen from Washington Co., Arkansas, USA). Females distinguished by clasper receptacle, in lateral aspect (Fig. 204), simple depression on lateral wall of segment X, bounded anteriorly by distinct declivity, with slight invagination at dorsal end of declivity; by clasper receptacle, in dorsal aspect (Fig. 205), simple, large, domed depression in lateral wall of segment X; and by sclerotised strap of vulval scale large, acute-triangular.

Biology.— The only available Canadian flight records are July 21-24, in southern Ontario. Ross (1944) gives flight records from April to September. He also indicates that larvae prefer smaller, clear streams of many riffles or rapids. Ross also concludes that this species adheres quite closely to the western fringes of the Oak-Hickory forest.

Distribution.— Recorded from Oklahoma and Kansas to southern Ontario (with gaps), with one record from Fraserburg, Ontario (Map 33).

Hydropsyche bidens Ross
Map 34; Fig. 206–212

Hydropsyche bidens Ross, 1938b:142; Denning, 1943:118; Ross, 1944:107; Schuster & Etnier, 1978:75.

Description.— Male fore-wing length 11.08 mm; pale brown, faintly irrorate, with darker areas along Cu1a-1b and A. Hind-wing hyaline. Antennae yellow-brown; basal ten flagellar annuli each with oblique, dark band. Vertex red-brown. Spurs pale brown. Thorax red-brown, to slightly paler laterally. Legs yellow-brown to straw.

Genitalia. Male. (Fig. 206–210). (Specimen from Ile Perrot, Québec). Males distinguished by wide, broadly rounded distal lobes of segment X, in lateral aspect (Fig. 206); by these lobes, in dorsal aspect (Fig. 207), separated by deep, narrow cleft with rounded interior expansion; and by distal article of clasper, in lateral aspect, slightly expanded at mid-point, then tapered sharply to dorsally curved, acuminate tooth (tooth visible in posterior aspect (Fig. 208)).

Genitalia. Female. (Fig. 211–212). (Specimen from Lac Monroe, Parc Mont Tremblant, Québec). Females distinguished by vulval scale with two sclerites (Fig. 211), one angled; by clasper receptacle high, ventrally tapered invagination, without inner opening visible (Fig. 211, 212); and by clasper receptacle dorsal end associated with thin, dark line originated postero-dorsad on segment X.

Biology.— Schuster & Etnier (1978) state that this is a species of larger rivers subject to heavy silt loading. They give flight season dates as April to September, concluding that there is only one generation per year.

Distribution.— Recorded from Montana, through Manitoba, to Québec, and south to Texas (Map 34). In Canada known only from southern Manitoba and southwestern Québec.

Hydropsyche californica Banks
Map 35; Fig. 213–219

Hydropsyche californica Banks, 1899:217; Betten, 1934:193; Milne, 1936:73; Ross, 1938c:16; Denning, 1943:115.
Hydropsyche scalaris Hagen; Milne, 1936:73 (as synonym of *H. californica*).

Description.— Male fore-wing length 9.44 mm; light chocolate-brown, faintly irrorate with larger hyaline areas peripherally. Hind-wing faintly tinted grey-brown. Antennae pale brown; basal seven flagellar annuli each with oblique, dark brown band (eight in female). Vertex very dark purplish brown, warts lighter. Spurs brownish yellow; lateral member

of middle leg pairs, and of hind-leg apical pair, notably shorter than mesal companions. Thorax very dark purplish brown, to dark chocolate-brown laterally.

Genitalia. Male. (Fig. 213–217). (Specimen from creek, Hwy 19, 32.5 km S of Kelsay Bay jct., Vancouver Island, British Columbia). Males distinguished by stout basal article of clasper in lateral aspect (Fig. 213); by distal article of clasper, in lateral aspect, offset somewhat posterad, of even width, with disto-ventral angle produced bluntly distad; by clasper, in posterior aspect (Fig. 215), smoothly curved mesad; and especially by distal lobes of tergum X, in dorsal aspect (Fig. 214), composite, with pair of secondary lobes within primary lobes.

Genitalia. Female. (Fig. 218–219). (Specimen from creek, Hwy 19, 32.5 km S of Kelsay Bay jct., Vancouver Island, British Columbia). Females distinguished by clasper receptacle small, boomerang-like, set high in lateral wall of segment X, in lateral aspect (Fig. 218); by lack of sclerotised strap on vulval scale; and by cercus thin, appressed to underside of dorsal lobe of segment XI, well separated from ventral lobe.

Biology.— Very little known. Two records from Canada available for flight season – one for July 10, the other simply for August. The July 10 material was taken by myself at a lake outlet into a middling-sized woodland creek over sandy boulder bottom.

Distribution.— Presently known from the western and northwestern cordilleran United States, and Vancouver Island, with a record from Minnesota (Map 35). In Canada this species is presently known only from two localities on Vancouver Island.

<center>

Hydropsyche dicantha Ross
Map 36; Fig. 220–226
</center>

Hydropsyche dicantha Ross, 1938b:146; Ross, 1944:102; Schuster & Etnier, 1978:80; Flint, Voshell, & Parker, 1979:845.

Description.— Male fore-wing length 7.72 mm; overall warm red-brown. Hind-wing very palely tinted reddish brown. Antennae deep red-brown; distal half of each flagellar annulus paler. Vertex red-brown. Spurs yellow-brown. Thorax deep red-brown, to paler laterally. Legs red-brown.

Genitalia. Male. (Fig. 220–224). (Specimen from Lac Monroe, Parc Mont Tremblant, Québec). Males distinguished by accuminate, hooked lobes on lateral faces of segment X (from which the species gets its name)(Fig. 220); by distal article of clasper rectangular in lateral aspect; and by large, sigmoid aedeagus (Fig. 223) with distal cleft narrowly v-shaped (Fig. 222).

Genitalia. Female. (Fig. 225–226). (Specimen from R. du Diable, Parc Mont Tremblant, Québec). Females distinguished by clasper receptacle, in lateral aspect (Fig. 225), extended across whole lateral wall of segment X, with posterior and anterior ventrally directed arms, comprised mostly of sharp declivity with very small invagination at postero-dorsal angle; by cercus of segment XI large, acute-triangular, directed postero-dorsad along with dorsal and ventral lobes; by cerci and associated lobes all visible in dorsal aspect (Fig. 226); and by sclerotised strap of vulval scale long, slender, widened distally, recurved.

Biology.— Schuster & Etnier (1978) indicate that larvae are fairly indiscriminate in choice of stream type, being known from small, cool, riffled streams, to large, warm rivers. Flight season extends from late June to late September. Canadian records are slightly earlier.

Distribution.— Presently known from Minnesota to Tennessee, to New Hampshire and southern Québec (Map 36). In Canada, recorded from southern fringes of Canadian Shield in Ontario and Québec, south to United States border.

<center>

Hydropsyche frisoni Ross
Map 37; Fig. 227–233
</center>

Hydropsyche frisoni Ross, 1938b:142; Ross, 1944:105; Schuster & Etnier, 1978:93.

Description.— Male fore-wing length 8.03 mm; light grey-brown, faintly irrorate overall. Hind-wing hyaline. Antennae yellow-brown; basal seven flagellar annuli each with oblique, dark band; presence of bands in faded paratype female uncertain. Vertex deep red-brown. Spurs yellow; lateral member of middle leg pairs shorter than mesal companions. Thorax deep red-brown. Legs light red-brown.

Genitalia. Male. (Fig. 227–231). (Specimen from Plateau Experimental Stn, Cumberland Co., Tennessee, USA). Males distinguished by distal article of clasper, in lateral aspect (Fig. 227), of uniform width, linear, with distal end tapered, curved dorsad as small median hook; by aedeagus, in lateral aspect (Fig. 230), with narrow base, distal half expanded, robust; by distal cleft of aedeagus narrow, v-shaped (Fig. 231); and by gap between distal lobes of tergum X, in dorsal aspect (Fig. 228) u-shaped.

Genitalia. Female. (Fig. 232–233). (Specimen from White R., Shoals, Indiana, USA – Paratype). Females distinguished by clasper receptacle as semi-circular declivity directed anterad, in lateral aspect (Fig. 232), with very slight invagination at dorsal end; and by sclerotised strap of vulval scale thin, dark line.

Biology.— Schuster & Etnier (1978) conclude that larvae prefer small, warm-water rivers and are intolerant of habitat alteration. Flight season is given as April through August.

Distribution.— Not yet known from Canada. Recorded from Minnesota to Missouri and Ohio in the United States (Map 37).

Hydropsyche hageni Banks
Map 38; Fig. 234–240

Hydropsyche hageni Banks, 1905a:14; Milne, 1936:73 (as synonym of *H. scalaris*); Denning, 1943:119; Ross, 1944:103; Schuster & Etnier, 1978:102; Flint, Voshell, & Parker, 1979:847.

Description.— Male fore-wing length 11.66 mm; dark grey-brown, faintly irrorate posterad of R1 (distally), with darker areas along veins. Hind-wing tinted grey-brown. Antennae bright pale red-brown; basal nine flagellar annuli each with oblique, dark band. Vertex red-brown. Spurs pale brown; lateral member of fore- and middle leg pairs shorter than mesal companions. Thorax red-brown. Legs pale red-brown.

Genitalia. Male. (Fig. 234–238). (Specimen from Clinch R., Hancock Co., Tennessee, USA). Males distinguished by basal article of clasper, in lateral aspect (Fig. 234), linear, of almost uniform width; by distal article of clasper irregular-pentagonal in outline; and by gap between distal lobes of tergum X, in dorsal aspect (Fig. 235), slightly narrower than interior, gap oval.

Genitalia. Female. (Fig. 239–240). (Specimen from Cahaba R., Bibb Co., Alabama, USA). Females distinguished by clasper receptacle small, narrow invagination at dorsal end of short declivity on lateral face of segment X (Fig. 239); by vulval scale with two sclerotised straps – one a fine, dark line, other wider, angled; and by ventral portion of clasper receptacle, in dorsal aspect (Fig. 240), overlapped by dorsal portion.

Biology.— The few Canadian records give a flight season of May 25 to June 26. Ross (1944) records flight from May to late August. Larvae appear to prefer faster parts of rivers over boulders and/or bedrock.

Distribution.— Recorded from Manitoba to Alabama, Virginia, and southeastern Ontario (Map 38). In Canada presently known only from eastern Manitoba, and southeastern Ontario.

Hydropsyche leonardi Ross
Map 39; Fig. 194–198

Hydropsyche leonardi Ross, 1938b:145; Ross, 1944:294; Flint, Voshell, & Parker, 1979:851.

Description.— Male fore-wing length 9.67 mm; orange-brown, with darker membrane about Cu1 + 2 and patches posterad of that vein. Hind-wing palely tinted light orange-brown. Antennae brown; some flagellar annuli with oblique, dark band, but number uncertain as most of flagellum missing. Vertex dark chocolate-brown. Spurs brown; lateral member of all pairs shorter than mesal companions. Thorax uniformly dark chocolate-brown. Legs light yellow-brown.

Genitalia. Male. (Fig. 194–198). (Specimen from Au Sable R., Crawford Co., Michigan, USA – Paratype). Males distinguished by large, splayed distal lobes of aedeagus, in dorsal aspect (Fig. 197); by distal lobes of tergum X separated by small, v-shaped notch, in dorsal aspect (Fig. 195); and by distal article of clasper, in lateral aspect (Fig. 194), robust, almost trapezoidal, with disto-ventral angle produced as small tooth, and with lateral face concave (see also Fig. 198).

Genitalia. Female. Unknown.

Biology.— Flint, Voshell, & Parker (1979) provide Virginia flight records which range from April 12 to October 20. Available Canadian records are May 20 and 29. The above authors report adult emergence from riffles of clean, fast-flowing larger rivers.

Distribution.— Presently known only from Michigan, Virginia, and southeastern Ontario (at Ottawa)(Map 39).

Hydropsyche occidentalis Banks
Map 40; Fig. 241–247

Hydropsyche occidentalis Banks, 1900:258; Betten, 1934:194; Milne, 1936:69, 71, 73; Ross, 1938c:17; Ross, 1944:294.
Hydropsyche novamexicana Banks, 1904b:110; Milne, 1936:73 (as synonym of *H. occidentalis*).

Description.— Male fore-wing length 8.50 mm; pale brownish yellow with scattered darker areas. Antennae yellow; at least basal six flagellar annuli each with oblique, dark band. Vertex pale reddish brown; yellow-brown in female. Spurs straw; lateral member of middle leg preapical pair notably shorter than mesal companion. Thorax pale reddish brown, to yellowish brown laterally. Legs yellow.

Genitalia. Male. (Fig. 241–245). (Specimen from Lethbridge, Alberta). Males distinguished by basal article of clasper with irregularly slender basal third; distal two-thirds parallel-sided, much wider in lateral aspect (Fig. 241); by distal article of clasper robust, in lateral aspect; by same article, in posterior aspect (Fig. 243), with disto-dorsal angle projected mesad from behind disto-ventral edge; and by gap between distal lobes of tergum X, in dorsal aspect (Fig. 242), wide, v-shaped, rounded, not angular.

Genitalia. Female. (Fig. 246–247). (Specimen from Lethbridge, Alberta). Females distinguished by clasper receptacle located very high on lateral wall of segment X – a simple slit (Fig. 246); by sclerotised strap of vulval scale linear, widened distally, of medium size; and by lobes of segment XI large, stubby, directed slightly postero-ventrad.

Biology.— From my records it seems that adults emerge from all manner of flowing waters, from small, weed-filled, plains streamlets to largest rivers, and from turbulent, rocky foothills streams and rivers. Flight season ranges from June 2 to August 19. Simmons *et al.* (1942) record larvae as being so numerous in a Sierra Nevada water conduit as to require shut-down for cleaning.

Distribution.— Widespread throughout western Cordillera from Mexico to British Columbia, east to Great Plains (at least in Canada) of Saskatchewan (Map 40). In Canada, recorded from south-central British Columbia to prairies and Boreal Forest of Alberta and Saskatchewan.

Hydropsyche orris Ross
Map 41; Fig. 248–254

Hydropsyche cornuta Ross, 1938b:141 (preoccupied by Martynov, 1909).
Hydropsyche orris Ross, 1938a:121 (new name); Denning, 1943:118; Ross, 1944:105; Schuster & Etnier, 1978:71.

Description.— Male fore-wing length 8.74 mm; pale red-brown; veins darker, foci for irroration pattern. Hind-wing tinted grey-brown. Antennae red-brown; basal 8-9 flagellar annuli each with oblique, dark band. Vertex deep red-brown; paler in available female. Spurs red-brown; lateral member of fore- and middle leg pairs much shorter than mesal companions. Thorax deep red-brown, to slightly paler laterally; warm red-brown in female. Legs red-brown, to straw distally.

Genitalia. Male. (Fig. 248–252). (Specimen from Washington Co., Arkansas, USA). Males distinguished by distal article of clasper, in lateral aspect (Fig. 248), of uniform width, curved slightly dorsad, with disto-ventral angle produced as acuminate tooth; by gap between distal lobes of tergum X, in dorsal aspect (Fig. 249), not deep, v-shaped; and by distal cleft of aedeagus (Fig. 252) shallow, v-shaped, continued basad by thin line of closure.

Genitalia. Female. (Fig. 253–254). (Specimen from Vicksburg, Mississippi, USA). Females distinguished by clasper receptacle small, triangular, in lateral aspect (Fig. 253), dorsally directed invagination of dorsal portion of semi-circular declivity of lateral wall of segment X; by cerci and dorsal lobes of segment XI, only, visible in dorsal aspect (Fig. 254); and by sclerotised strap of vulval scale narrow at each end, irregularly widened in middle.

Biology.— Schuster & Etnier (1978) conclude that larvae are adapted to large rivers with high silt loading and high concentration of suspended organic matter. They also conclude that the species is univoltine, with flight season from April to October.

Distribution.— Presently known from South Dakota to Texas, Georgia, and Michigan (Map 41). Not yet known from Canada.

Hydropsyche phalerata Hagen
Map 42; Fig. 255–261

Hydropsyche phalerata Hagen, 1861:287; Betten, 1934:189; Milne, 1936:73 (as synonym of *H. morosa*); Denning, 1943:113; Ross, 1944:102; Schuster & Etnier, 1978:78; Flint, Voshell, & Parker, 1979:853.

Description.— Male fore-wing length 7.72 mm; pale grey-brown, no evident pattern. Hind-wing hyaline, to faintly tinted. Antennae deep red-brown; basal eight flagellar annuli each with oblique, dark band. Vertex deep brown. Spurs yellow-brown; lateral member of middle leg pairs shorter than mesal companions. Thorax deep brown, to mixed deep brown and paler brown laterally. Legs yellow-brown, to straw laterally.

Genitalia. Male. (Fig. 255–259). (Specimen from Mississippi R., Hennepin Co., Minnesota, USA). Males distinguished by distal lobes of tergum X narrow, directed postero-dorsad in lateral aspect (Fig. 255), with gap between, in dorsal aspect (Fig. 256); by distal cleft of aedeagus, in dorsal aspect (Fig. 259), v-shaped, narrow, of medium depth; and by distal article of clasper with dorsal edge straight, ventral edge sinuate, with disto-ventral angle slightly, bluntly produced in lateral aspect (Fig. 255).

Genitalia. Female. (Fig. 260–261). (Specimen from Mississippi R., Hennepin Co., Minnesota, USA). Females distinguished by clasper receptacle small, triangular, located very close to anterior edge of segment X, in lateral aspect (Fig. 260); by ventral lobe of segment XI well ventrad of cercus and dorsal lobe; and by sclerotised strap of vulval scale thin, dark line deeply bowed ventrad.

Biology.— Flint, Voshell, & Parker (1979) give a flight season range of May 25 to September 27, in Virginia. Ross (1944) gives the Illinois range as late April to September. According to Schuster & Etnier (1978) larvae prefer very wide rivers with shallow riffle areas, with silty gravel and small-to-medium-sized rock bottom, with high suspended organic loading, and with warm water conditions in late Spring and early Fall.

Distribution.— Though recorded from Kansas, this species is primarily confined east of a line from Minnesota to Florida (Map 42), as far east as Massachusetts and southern Québec. In Canada it is presently known only from southern Québec and southern Ontario.

Hydropsyche placoda Ross
Map 43; Fig. 262–268

Hydropsyche placoda Ross, 1941:87; Denning, 1943:115; Ross, 1944:103; Schuster & Etnier, 1978:127.

Description.— Male fore-wing length 8.66 mm; tinted translucent brown, with darker colour mostly about R1 and between Cu1+2 to A3. Female rather darker overall. Antennae pale orange-brown; basal eight flagellar annuli each with oblique, dark band. Vertex orange-brown, markedly narrowed due to considerable enlargement of compound eyes; eyes normal in female. Spurs yellow; lateral member of middle leg pairs notably shorter than mesal companions. Spur formula apparently 1,4,4. Thorax orange-brown, to yellow-brown laterally. Legs pale brown to straw.

Genitalia. Male. (Fig. 262–266). (Specimen from Pembina R., Sangudo, Alberta). Males distinguished by distal article of clasper, in lateral aspect (Fig. 262), rectangular, with distal edge scalloped; by gap between distal lobes of tergum X v-shaped, wide, shallow in dorsal aspect (Fig. 263); and by distal cleft of aedeagus, in dorsal aspect (Fig. 265), v-shaped, deep, very narrow.

Genitalia. Female. (Fig. 267–268). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Females distinguished by clasper receptacle simple, circular pit anterad of long, curved declivity very close to anterior edge of segment X (Fig. 267).

Biology.— Flight season in Canada ranges from May 25 to September 5. Little more known at present. The species is recorded from St Lawrence R. at Montréal, where are rapids of a very large river.

Distribution.— Presently known from Alberta and Montana east to Illinois, New York State, and Québec (Map 43). In Canada it is known from both Boreal Forest and prairies of the three Prairie Provinces, and from St Lawrence R. valley of Ontario and Québec.

Hydropsyche rossi Flint, Voshell, & Parker
Map 44; Fig. 269–275

Hydropsyche incommoda (not Hagen): Ross, 1944:106; Schuster & Etnier, 1978:92.
Hydropsyche rossi Flint, Voshell, & Parker, 1979:854.

Description.— Male fore-wing length 9.67 mm; grey-brown, irrorate overall. Hind-wing hyaline. Antennae pale brown; basal nine flagellar annuli each with oblique, dark band. Vertex yellow-brown; warts darker in female. Spurs with lateral member of middle leg pairs shorter than mesal companions. Thorax deep red-brown, to deep yellow-brown laterally. Legs yellow. All warts darker in female.

Genitalia. Male. (Fig. 269–273). (Specimen from Waterford, Marshall Co., Mississippi, USA – Paratype). Males distinguished by distal article of clasper with ventral edge linear, dorsal edge sinuate, disto-ventral angle with short, curved tooth (Fig. 269); by postero-dorsal corner of distal lobe of tergum X angled (Fig. 269); and by gap between distal lobes, in dorsal aspect (Fig. 270), small, narrower at opening, elliptical in outline.

Genitalia. Female. (Fig. 274–275). (Specimen from Waterford, Marshall Co., Mississippi, USA – Paratype). Females distinguished by clasper receptacle, in lateral aspect (Fig. 274), located dorso-anterad on lateral wall of segment X, small, with outer margin anterior end much lower than posterior end, with no visible inner opening, with two curved grooves on floor of receptacle; and by sclerotised strap of vulval scale small, acute-triangular, with thin, dark line from apex to base of segment X – also, small secondary sclerite dorsad of primary.

Biology.— Flight season ranges from March 23 to September 25 according to Flint, Voshell, & Parker (1979), with reference to States from Illinois south to Arkansas. If this species is found in Canada the range may be expected to be rather shortened, especially in Spring. Little more known.

Distribution.— Not yet known from Canada. Recorded in United States from area bounded by Missouri to Florida, Virginia, and Illinois (Map 44).

Hydropsyche scalaris Hagen
Map 45; Fig. 276–282

Hydropsyche scalaris Hagen, 1861:286; Betten, 1934:190; Milne, 1936:69, 72, 73; Denning, 1943:112; Ross, 1944:106; Schuster & Etnier, 1978:87; Flint, Voshell, & Parker, 1979:856.

Description.— Male fore-wing length 11.08 mm; pale reddish brown, faintly irrorate, with darker areas along veins – especially Cu1 and A3. Antennae yellow-brown; basal nine flagellar annuli each with oblique, dark band. Vertex yellow-brown. Spurs pale yellow-brown; lateral member of middle leg pairs, and hind-leg apical pair notably shorter than mesal companions. Thorax deep orange-brown, to paler laterally. Legs pale brown to straw.

Genitalia. Male. (Fig. 276–280). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Males distinguished by distal article of clasper, in lateral aspect (Fig. 276), much like knife blade; by distal cleft of aedeagus deep, narrow, with widening part-way along length, in dorsal aspect (Fig. 280); and by gap between distal lobes of tergum X, in dorsal aspect (Fig. 277), narrow, slightly widened interiorly.

Genitalia. Female. (Fig. 281–282). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Females distinguished by clasper receptacle, in lateral aspect (Fig. 281), with sharp declivity ventrad of anterior end of outer margin of receptacle, with posterior end of margin continued to dorsum of segment X by thin, dark line; by inner opening of receptacle not evident in lateral aspect, inner end of receptacle curved slightly dorso-posterad; and by ventral portion of receptacle, in dorsal aspect (Fig. 282), overlapped by dorsal portion – inner opening visible.

Biology.— Canadian flight season records range from June 4 to August 28. In Virginia, Flint, Voshell, & Parker (1979) recorded adults from May 21 to October 20. Schuster & Etnier (1978) have little more to report on this species except to conclude that larvae prefer warmer water streams of various sizes.

Distribution.— Recorded from Colorado and New Mexico to Georgia, Maine, and southern Québec (Map 45). In Canada, known primarily from southern Québec and Ontario, but there is one isolated record from Duck Mountain area of Manitoba, which is in the Boreal Forest.

Hydropsyche simulans Ross
Map 46; Fig. 283–289

Hydropsyche simulans Ross, 1938b:139; Denning, 1943:117; Ross, 1944:104; Schuster & Etnier, 1978:90.

Description.— Male fore-wing length 10.37 mm; warm yellowish brown, uniformly irrorate except from distal end of thyridial cell to f1-f5. Antennae pale yellow-brown; basal ten flagellar annuli each with oblique, dark band; basal nine in female. Vertex yellow-brown. Spurs yellow; lateral member of middle and hind-leg pairs notably shorter than mesal companions. Thorax red-brown dorsally except mesal line yellow; laterally yellow-brown. Legs yellow to straw.

Genitalia. Male. (Fig. 283–287). (Specimen from Mt Carmel, Illinois, USA – Paratype). Males distinguished by distal lobes of tergum X, in lateral aspect (Fig. 283), square; by these distal lobes, in dorsal aspect (Fig. 284), with gap between circular; and by distal article of clasper like knife blade in lateral aspect.

Genitalia. Female. (Fig. 288–289). (Specimen from Washington Co., Arkansas,USA). Females distinguished by outer margin of clasper receptacle, in lateral aspect (Fig. 288), continued ventrad by declivity, dorsad by thin, dark line; by inner end of receptacle acuminate in lateral aspect, directed dorso-posterad; by sclerotised strap of vulval scale thin, very little widened distally; and by ventral area of clasper receptacle, in dorsal aspect (Fig. 289), slightly overlapped by dorsal area.

Biology.— Ross (1944) records emergence as April to late September. Schuster & Etnier (1978) conclude that larvae prefer larger rivers (30-60 m width) with boulder and coarse gravel bottom intermixed with silt. They seem to prefer streams with high organic content.

Distribution.— Known to occur from Montana south to Texas, east to southern Ontario (Map 46), this species is known in Canada from one locality near Sarnia, Ontario.

Hydropsyche valanis Ross
Map 47; Fig. 290–296

Hydropsyche valanis Ross, 1938b:144; Ross, 1944:105; Schuster & Etnier, 1978:85.

Description.— Male fore-wing length 8.35 mm; warm red-brown, no evident pattern; faintly irrorate in female. Antennae yellow-brown; basal seven flagellar annuli each with oblique, dark band. Vertex dull yellow-brown, narrow; compound eyes large, with dorso-mesal edges slanted anterad in dorsal aspect; vertex and eyes normal in female. Spurs straw; lateral member of middle and hind-leg pairs notably shorter than mesal companions. Thorax uniformly dull red-brown (dull yellow-brown in female). Legs red-brown, to straw distally; yellow-brown to straw in female.

Genitalia. Male. (Fig. 290–294). (Specimen from Baker, Illinois, USA). Males distinguished by distal article of clasper, in lateral aspect (Fig. 290), relatively narrow, with tip curved dorsad from entire width of article; by gap between distal lobes of tergum X, in dorsal aspect (Fig. 291), wide, composite, with inner portion u-shaped; and by distal cleft of aedeagus, in dorsal aspect (Fig. 294), complex, with four separate modifications throughout its depth.

Genitalia. Female. (Fig. 295–296). (Specimen from Pontiac, Illinois, USA). Females distinguished by clasper receptacle outer margin with distinct tooth close to posterior end of margin, in lateral aspect (Fig. 295); by receptacle directed dorso-anterad, without inner opening; and by only dorsal lobes of segment XI visible in dorsal aspect (Fig. 296).

Biology.— Ross (1944) indicates flight season lasts from May to late August. Little more known, but larvae may prefer very large, warm rivers (see Schuster & Etnier, 1978:86).

Distribution.— Known from Minnesota to Kentucky and Ohio; not yet recorded from Canada.

Hydropsyche venularis Banks
Map 48; Fig. 297–303

Hydropsyche venularis Banks, 1914:252; Betten, 1934:524; Milne, 1936:73 (as synonym of *H. scalaris*); Ross, 1944:294; Schuster & Etnier, 1978:96.

Description.— Male fore-wing length 9.98 mm; warm red-brown, faintly irrorate distally; veins Cu1+2 and A darker. In female, irrorate between R1 and RS also. Antennae yellow-brown; basal nine flagellar annuli each with oblique, dark band; eight in female. Vertex yellow-brown, narrow, eyes larger than in other species; female normal. Spurs yellow; lateral member of middle leg pairs shorter than mesal companions. Thorax yellow-brown, to red-brown laterally. Legs straw-coloured.

Genitalia. Male. (Fig. 297–301). (Specimen from Conasauga R., Bradley Co., Tennessee, USA). Males distinguished by distal article of clasper, in lateral aspect (Fig. 297), with disto-dorsal corner toothed; by distal lobes of tergum X

rounded-triangular in lateral aspect; and by these distal lobes, in dorsal aspect (Fig. 298), separated by flared, v-shaped gap.

Genitalia. Female. (Fig. 302–303). (Specimen from Conasauga R., Bradley Co., Tennessee, USA). Females distinguished by clasper receptacle represented by depression on lateral wall of segment X (Fig. 302); by this depression bounded anteriorly by declivity; and by vulval scale with angled secondary sclerotised strap on side, besides narrow, short, primary strap.

Biology.— Larvae occur in medium-sized rivers with large riffle areas; they seem to prefer vegetation-covered rocks. No flight records available.

Distribution.— Recorded from area bounded by Wisconsin, Missouri, Georgia, and New York (Map 48). Not yet known from Canada.

Map 31. Known distribution of *Hydropsyche aerata* Ross in North America, by state.
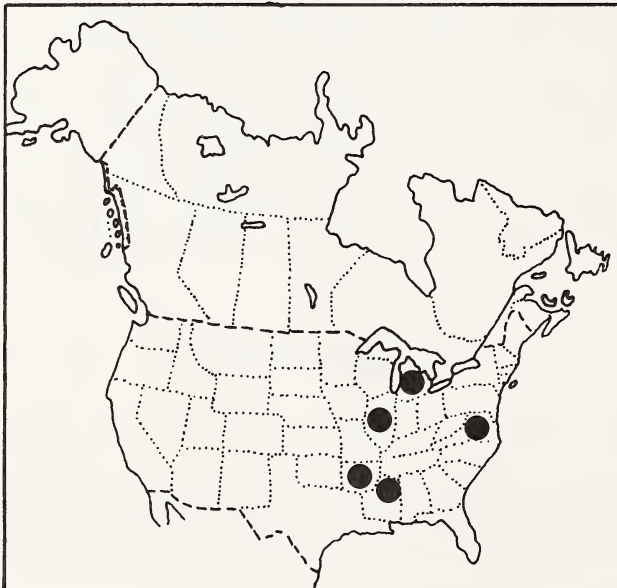
Map 32. Known distribution of *Hydropsyche alvata* Denning in North America, by state.
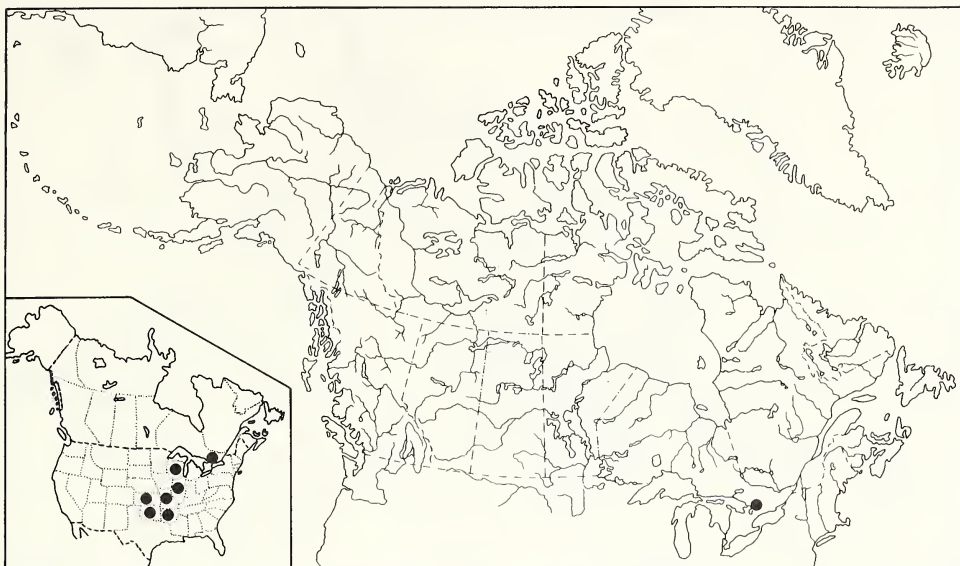
Map 33. Collection localities for *Hydropsyche arinale* Ross in Canada, with known distribution in North America by state or province.
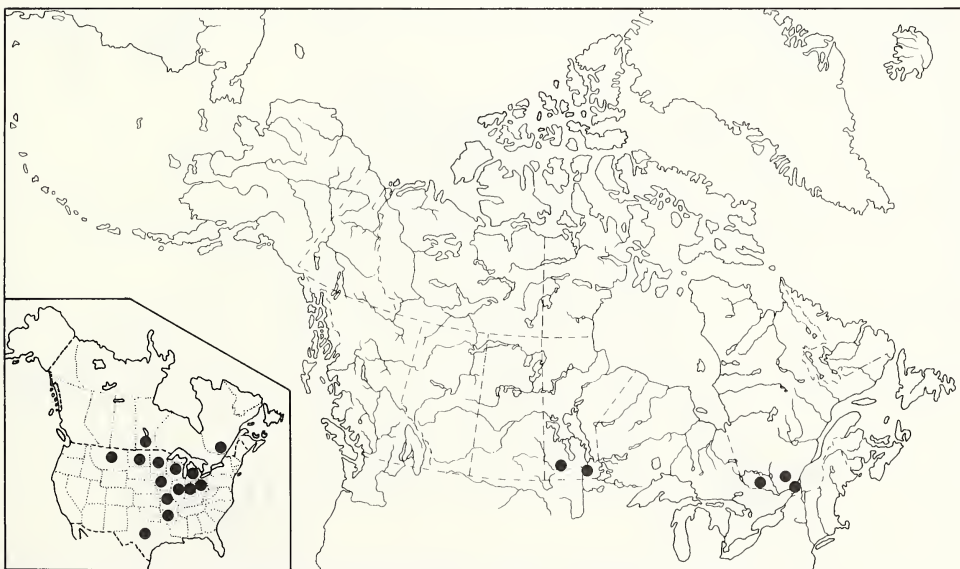
Map 34. Collection localities for *Hydropsyche bidens* Ross in Canada, with known distribution in North America by state or province.

Map 35. Collection localities for *Hydropsyche californica* Banks in Canada, with known distribution in North America by state or province.
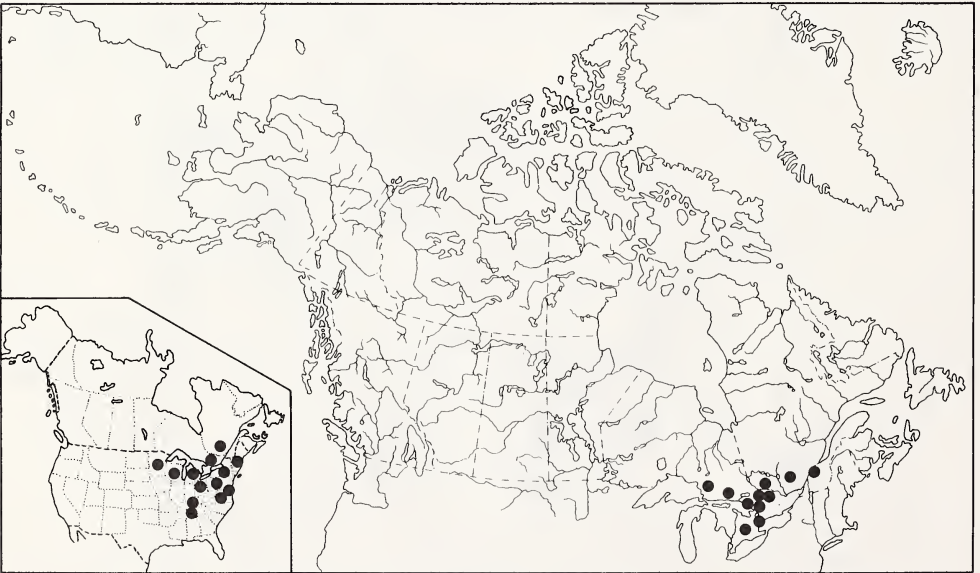
Map 36. Collection localities for *Hydropsyche dicantha* Ross in Canada, with known distribution in North America by state or province.
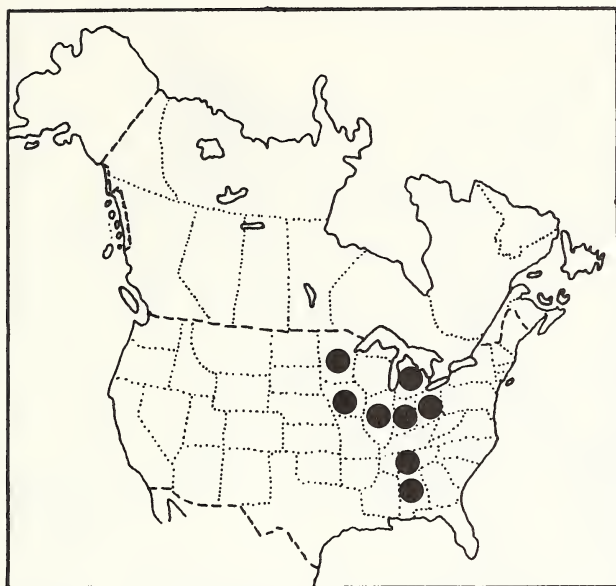
Map 37. Known distribution of *Hydropsyche frisoni* Ross in North America, by state.
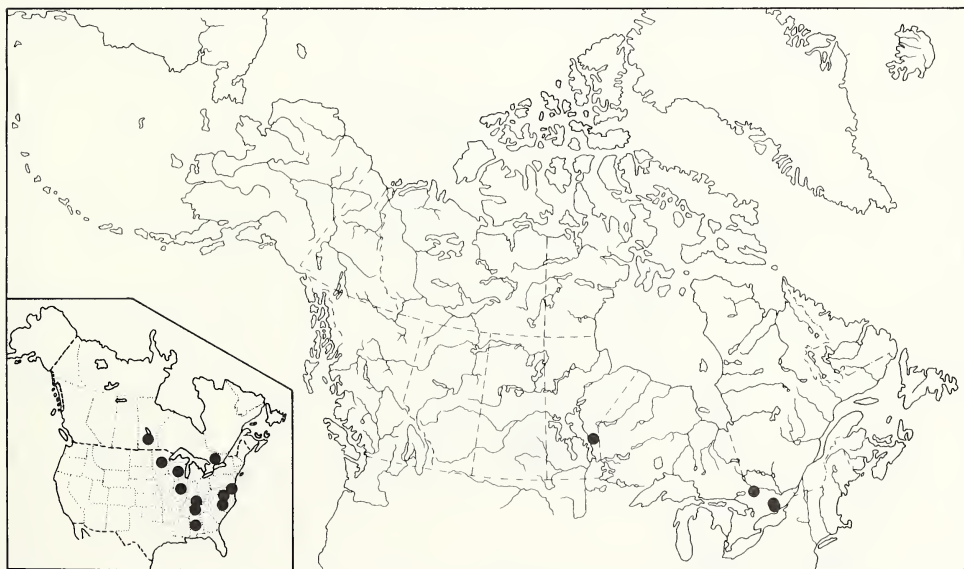
Map 38. Collection localities for *Hydropsyche hageni* Banks in Canada, with known distribution in North America by state or province.

Map 39. Collection localities for *Hydropsyche leonardi* Ross in Canada, with known distribution in North America by state or province.
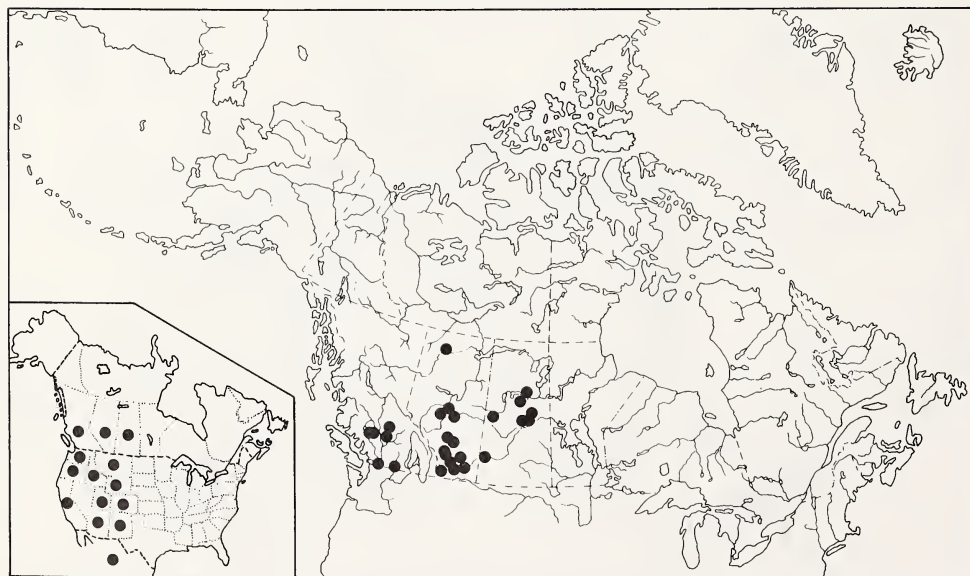
Map 40. Collection localities for *Hydropsyche occidentalis* Banks in Canada, with known distribution in North America by state or province.
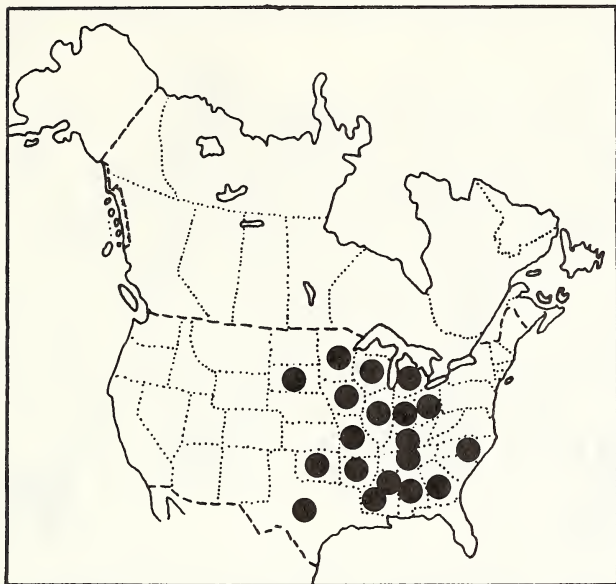
Map 41. Known distribution of *Hydropsyche orris* Ross in North America, by state.
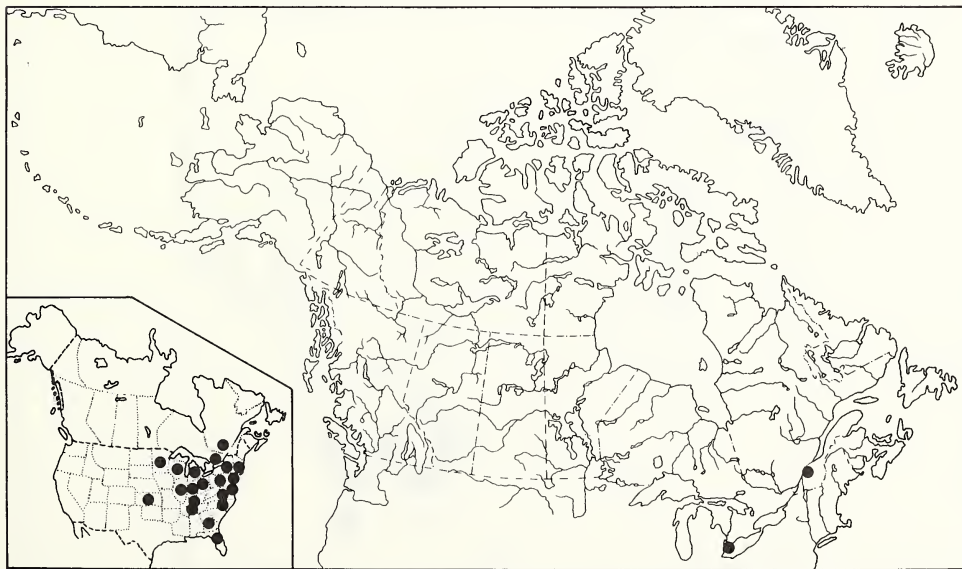
Map 42. Collection localities for *Hydropsyche phalerata* Hagen in Canada, with known distribution in North America by state or province.
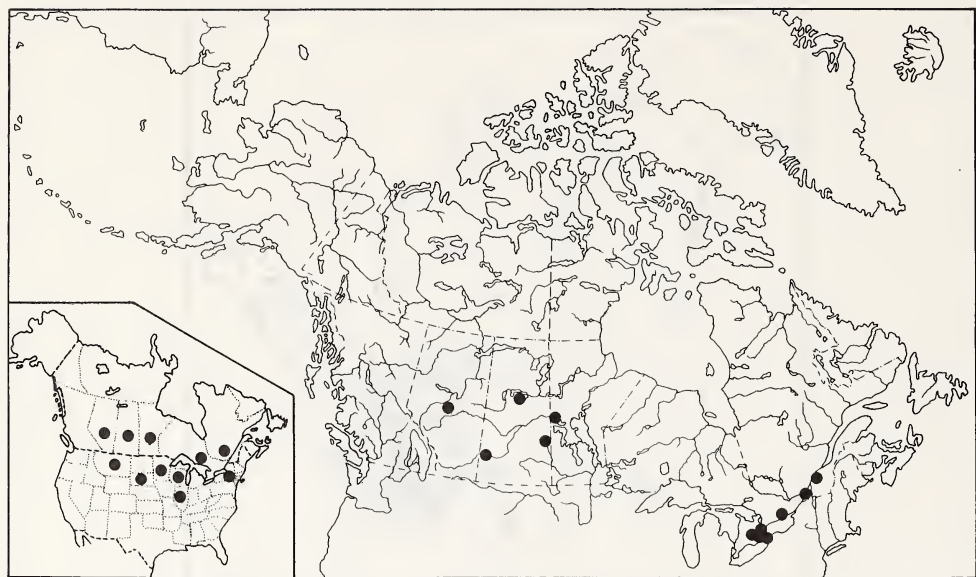
Map 43. Collection localities for *Hydropsyche placoda* Ross in Canada, with known distribution in North America by state or province.

Map 44. Known distribution of *Hydropsyche rossi* in North America, by state.
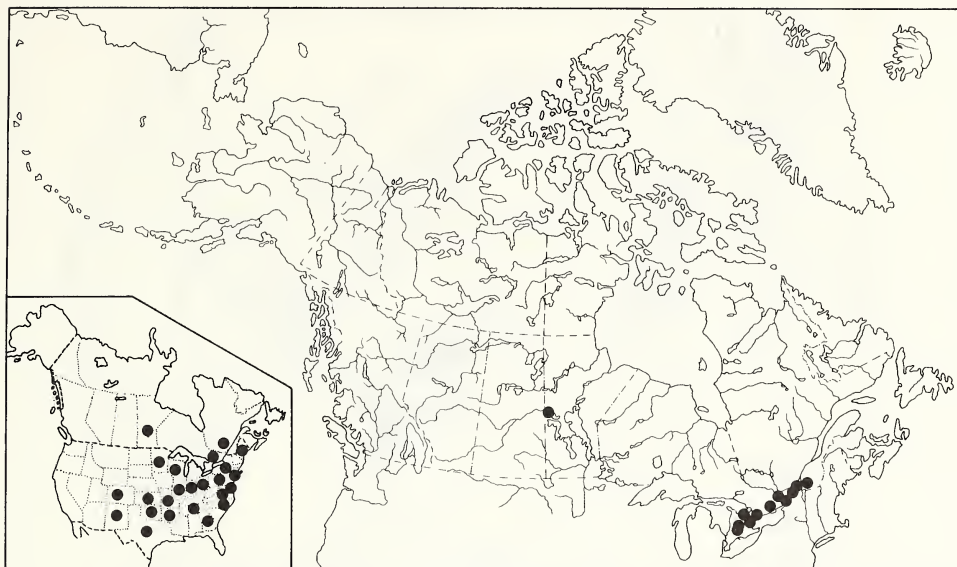
Map 45. Collection localities for *Hydropsyche scalaris* Hagen in Canada, with known distribution in North America by state or province.
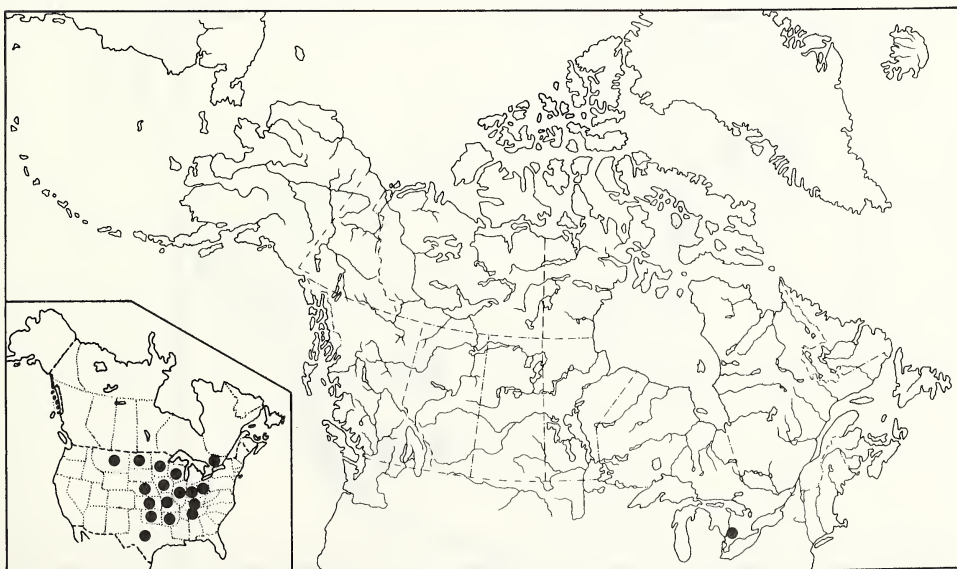
Map 46. Collection localities for *Hydropsyche simulans* Ross in Canada, with known distribution in North America by state or province.
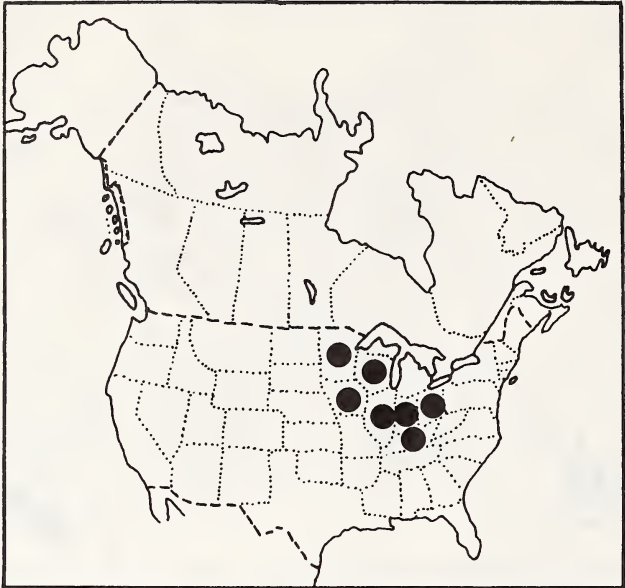
Map 47. Known distribution of *Hydropsyche valanis* Ross in North America, by state.
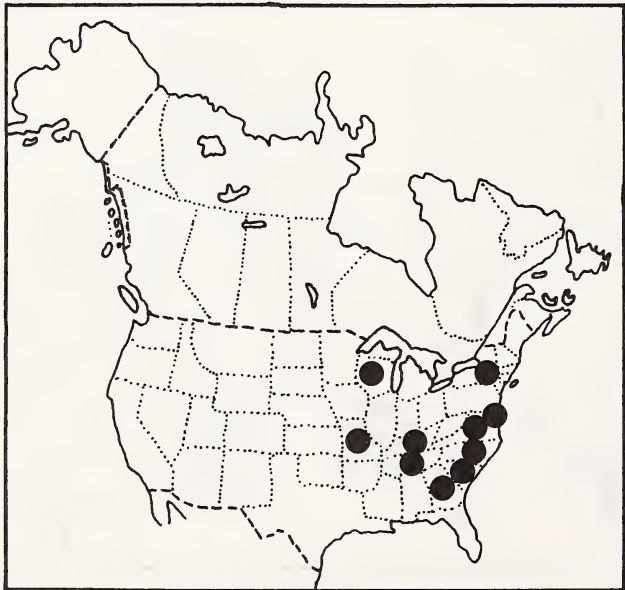
Map 48. Known distribution of *Hydropsyche venularis* Banks in North America, by state.

Fig. 182–188, *Hydropsyche aerata* Ross: 182, genital capsule of male, lateral aspect; 183, genital capsule of male, dorsal aspect; 184, left clasper of male, posterior aspect; 185, aedeagus of male, lateral aspect; 186, aedeagus of male, dorsal aspect of tip; 187, genital segments of female, lateral aspect; 188, genital segments of female, dorsal aspect. pr, preanal appendage; cr, clasper receptacle; ce, cercus; vs, vulval scale.
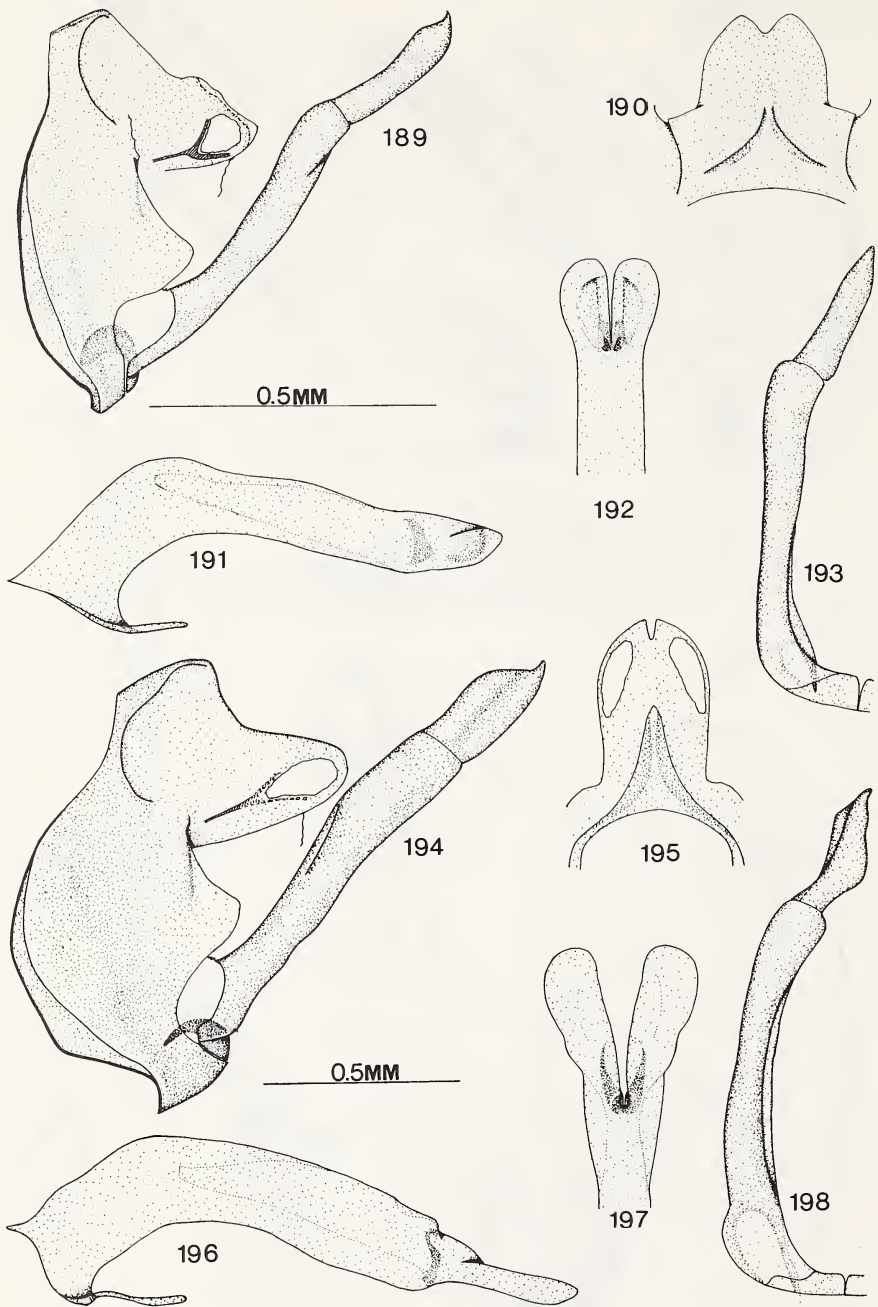
Fig. 189–198. 189–193, *Hydropsyche alvata* Denning: 189, genital capsule of male, lateral aspect; 190, genital capsule of male, dorsal aspect; 191, aedeagus of male, lateral aspect; 192, aedeagus of male, dorsal aspect of tip; 193, left clasper of male, posterior aspect. 194–198, *Hydropsyche leonardi* Ross: 194, genital capsule of male, lateral aspect; 195, genital capsule of male, dorsal aspect; 196, aedeagus of male, lateral aspect; 197, aedeagus of male, dorsal aspect of tip; 198, left clasper of male, posterior aspect.

Fig. 199–205, *Hydropsyche arinale* Ross: 199, genital capsule of male, lateral aspect; 200, genital capsule of male, dorsal aspect; 201, left clasper of male, posterior aspect; 202, aedeagus of male, lateral aspect; 203, aedeagus of male, dorsal aspect of tip; 204, genital segments of female, lateral aspect; 205, genital segments of female, dorsal aspect.

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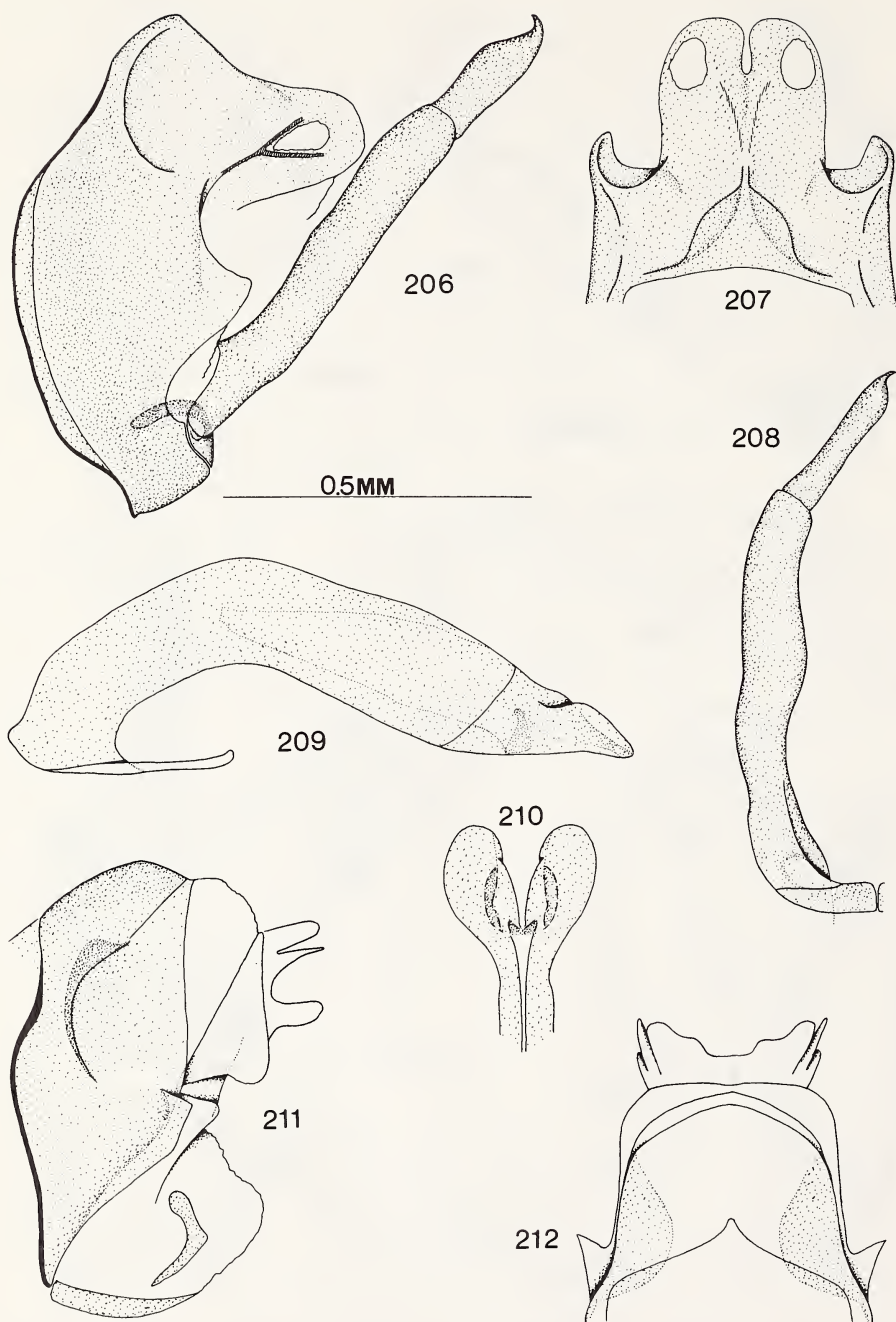
Fig. 206–212, *Hydropsyche bidens* Ross: 206, genital capsule of male, lateral aspect; 207, genital capsule of male, dorsal aspect; 208, left clasper of male, posterior aspect; 209, aedeagus of male, lateral aspect; 210, aedeagus of male, dorsal aspect of tip; 211, genital segments of female, lateral aspect; 212, genital segments of female, dorsal aspect.
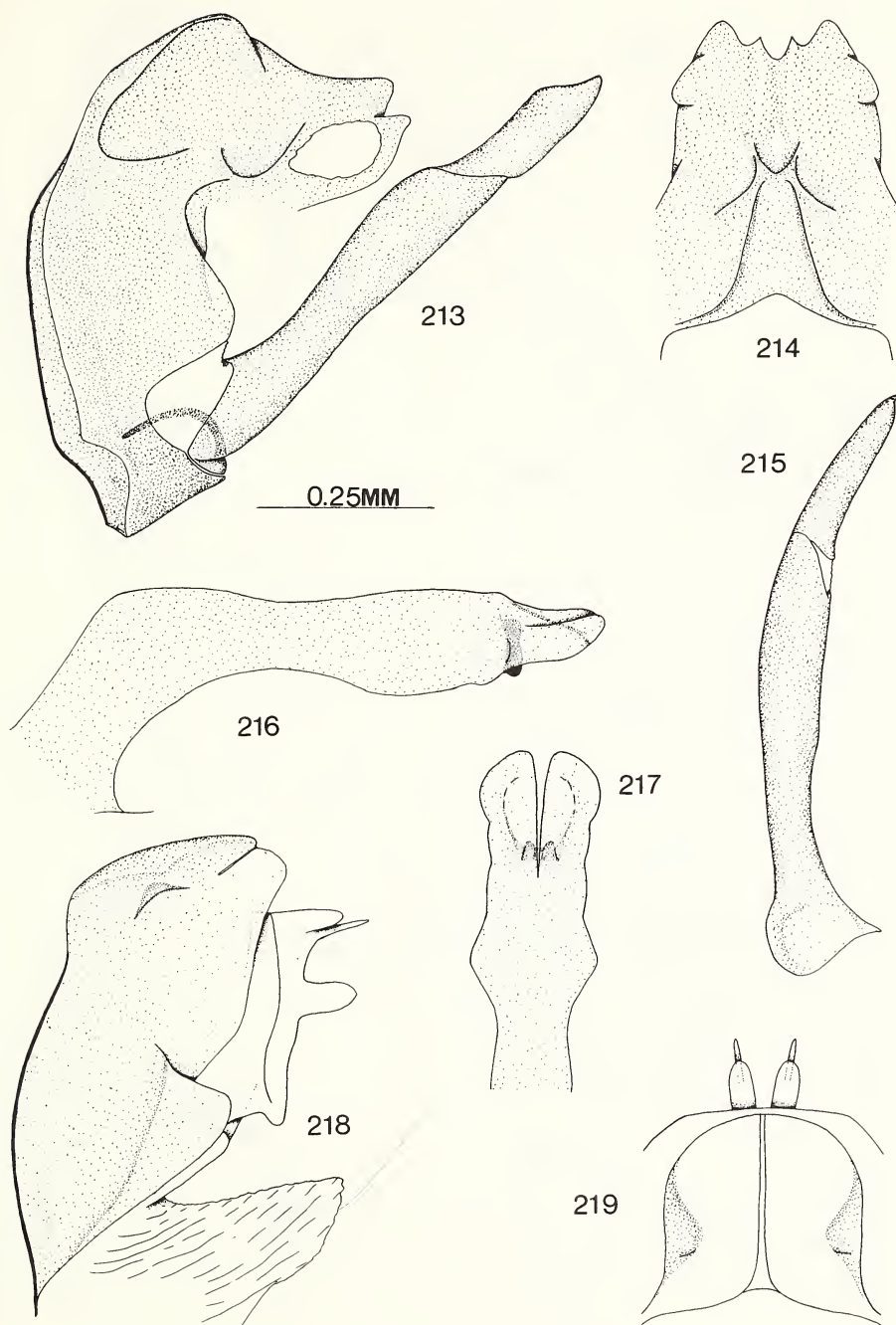
Fig. 213–219, *Hydropsyche californica* Banks: 213, genital capsule of male, lateral aspect; 214, genital capsule of male, dorsal aspect; 215, left clasper of male, posterior aspect; 216, aedeagus of male, lateral aspect; 217, aedeagus of male, dorsal aspect of tip; 218, genital segments of female, lateral aspect; 219, genital segments of female, dorsal aspect.
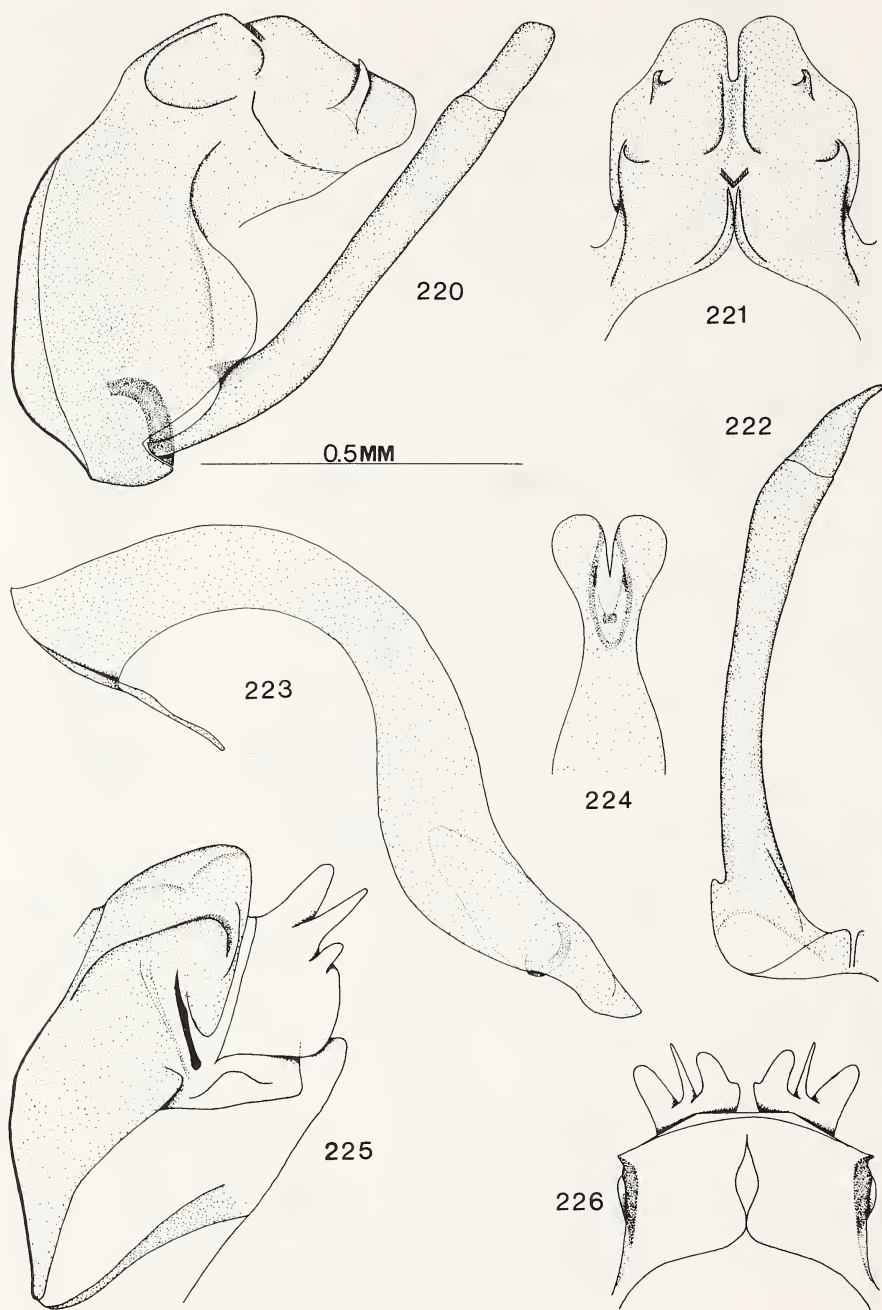
Fig. 220–226, *Hydropsyche dicantha* Ross: 220, genital capsule of male, lateral aspect; 221, genital capsule of male, dorsal aspect; 222, left clasper of male, posterior aspect; 223, aedeagus of male, lateral aspect; 224, aedeagus of male, dorsal aspect of tip; 225, genital segments of female, lateral aspect; 226, genital segments of female, dorsal aspect.

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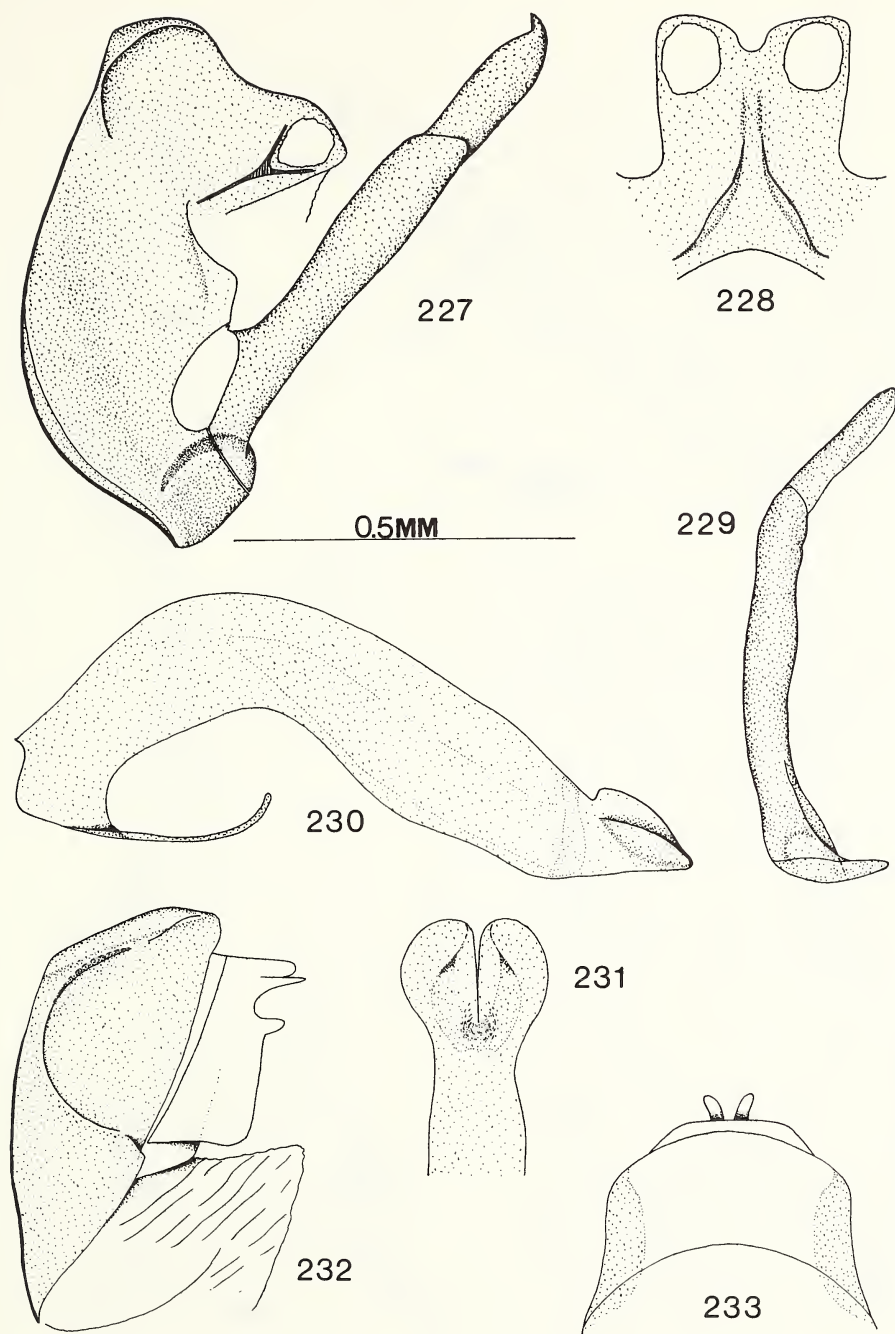
Fig. 227–233, *Hydropsyche frisoni* Ross: 227, genital capsule of male, lateral aspect; 228, genital capsule of male, dorsal aspect; 229, left clasper of male, posterior aspect; 230, aedeagus of male, lateral aspect; 231, aedeagus of male, dorsal aspect of tip; 232, genital segments of female, lateral aspect; 233, genital segments of female, dorsal aspect.
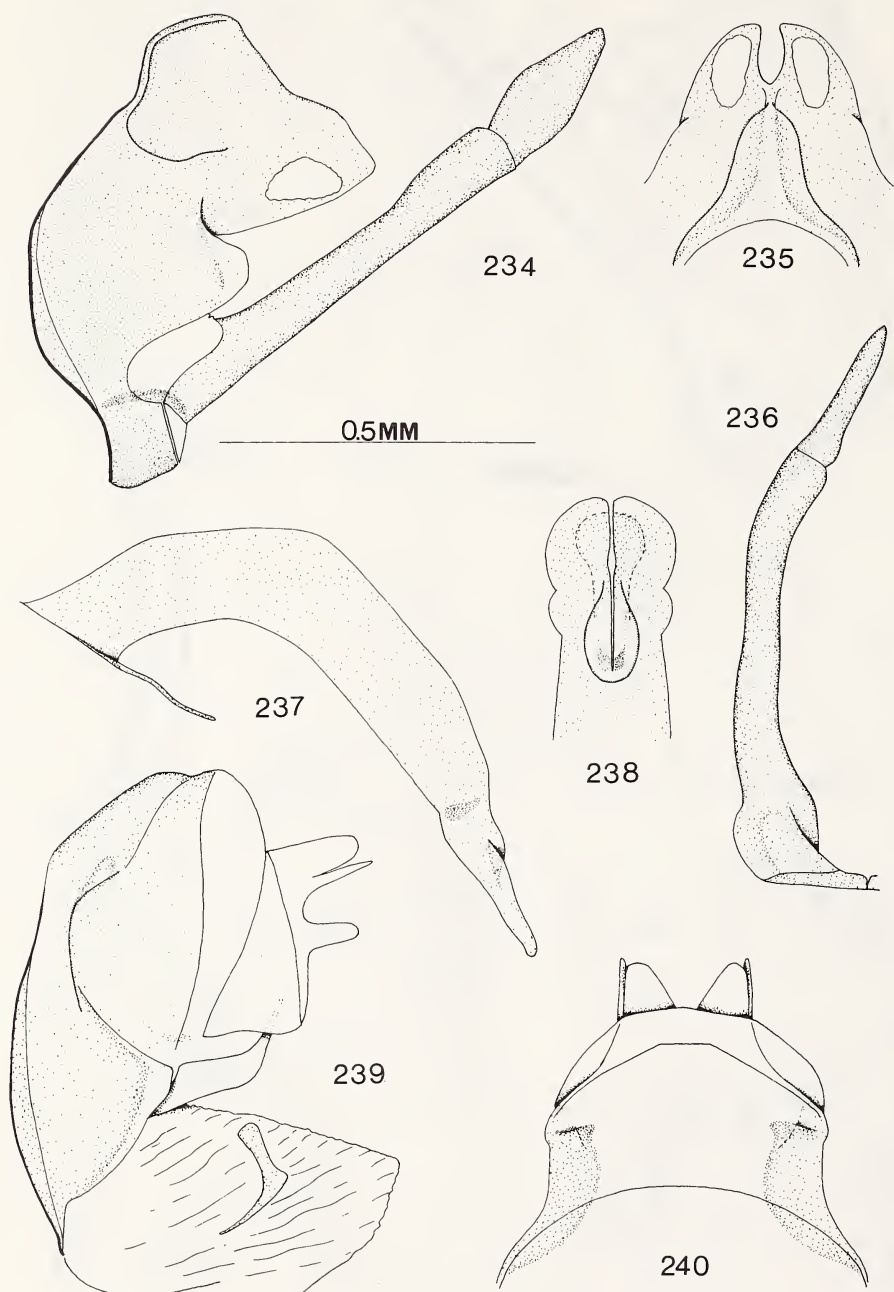
Fig. 234–240, *Hydropsyche hageni* Banks: 234, genital capsule of male, lateral aspect; 235, genital capsule of male, dorsal aspect; 236, left clasper of male, posterior aspect; 237, aedeagus of male, lateral aspect; 238, aedeagus of male, dorsal aspect of tip; 239, genital segments of female, lateral aspect; 240, genital segments of female, dorsal aspect.
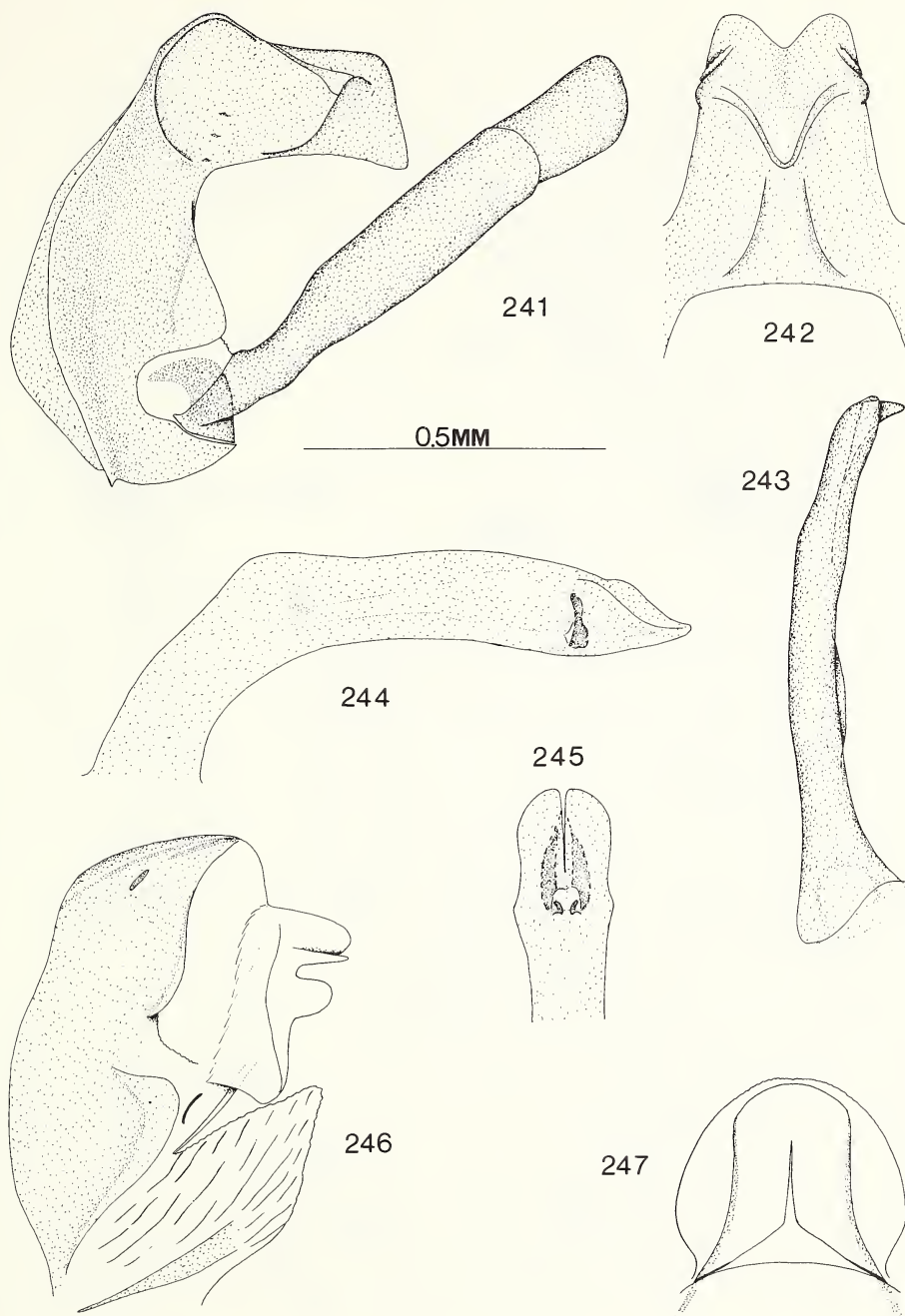
Fig. 241–247, *Hydropsyche occidentalis* Banks: 241, genital capsule of male, lateral aspect; 242, genital capsule of male, dorsal aspect; 243, left clasper of male, posterior aspect; 244, aedeagus of male, lateral aspect; 245, aedeagus of male, dorsal aspect of tip; 246, genital segments of female, lateral aspect; 247, genital segments of female, dorsal aspect.
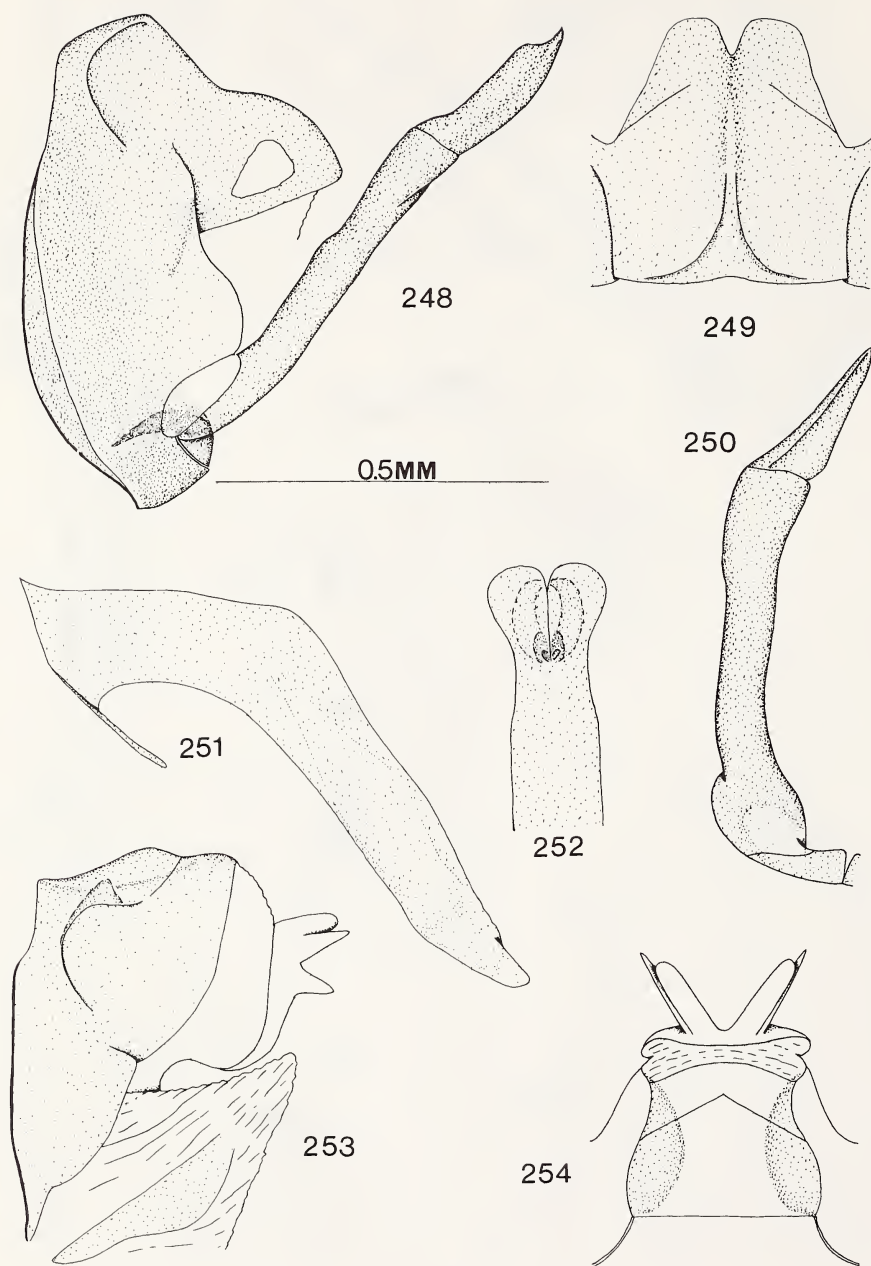
Fig. 248–254, *Hydropsyche orris* Ross: 248, genital capsule of male, lateral aspect; 249, genital capsule of male, dorsal aspect; 250, left clasper of male, posterior aspect; 251, aedeagus of male, lateral aspect; 252, aedeagus of male, dorsal aspect of tip; 253, genital segments of female, lateral aspect; 254, genital segments of female, dorsal aspect.
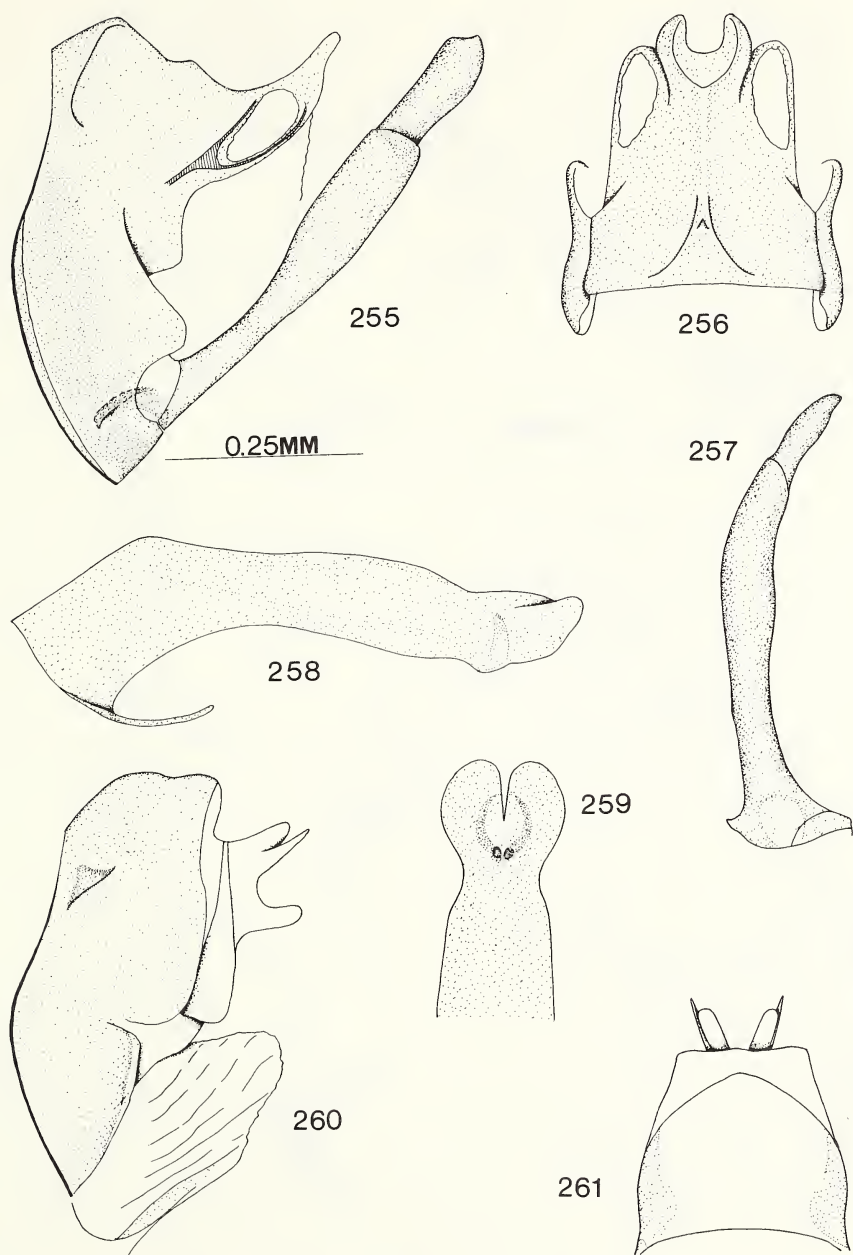
Fig. 255–261, *Hydropsyche phalerata* Hagen: 255, genital capsule of male, lateral aspect; 256, genital capsule of male, dorsal aspect; 257, left clasper of male, posterior aspect; 258, aedeagus of male, lateral aspect; 259, aedeagus of male, dorsal aspect of tip; 260, genital segments of female, lateral aspect; 261, genital segments of female, dorsal aspect.
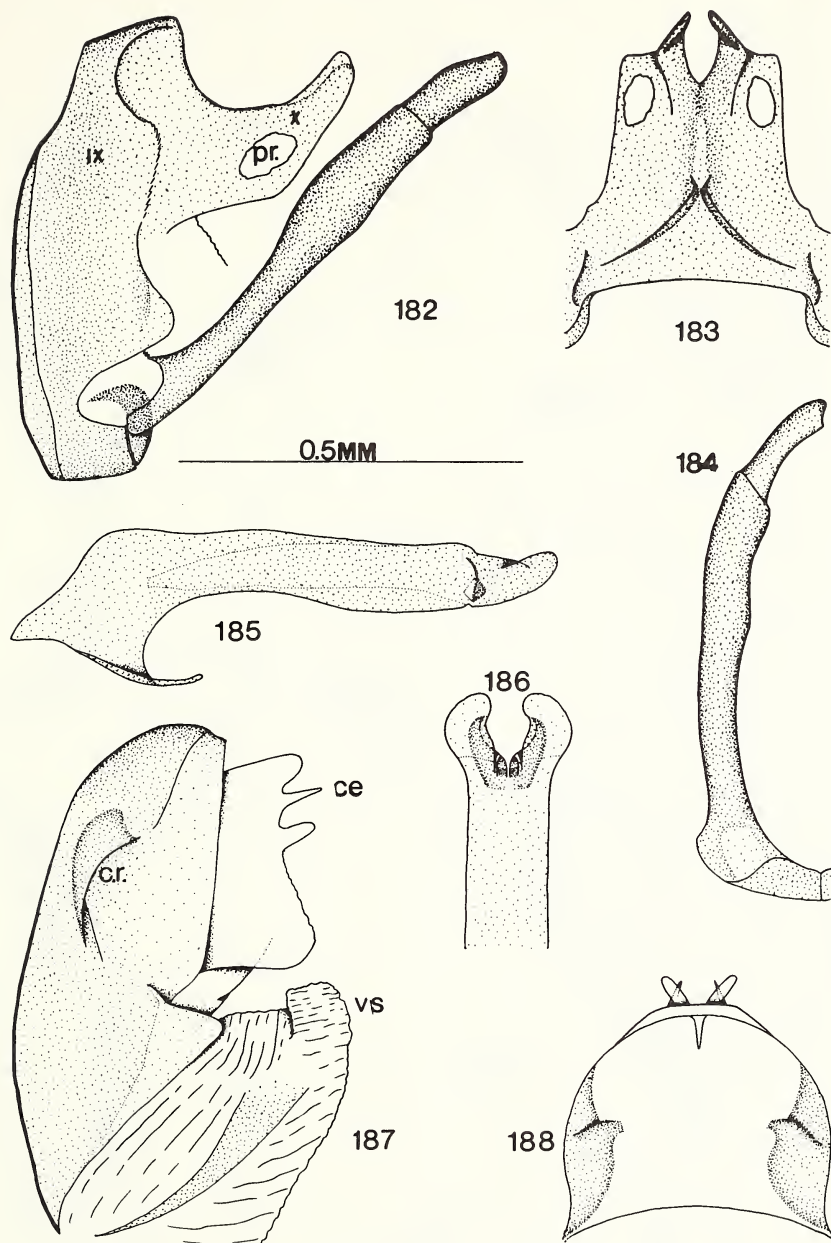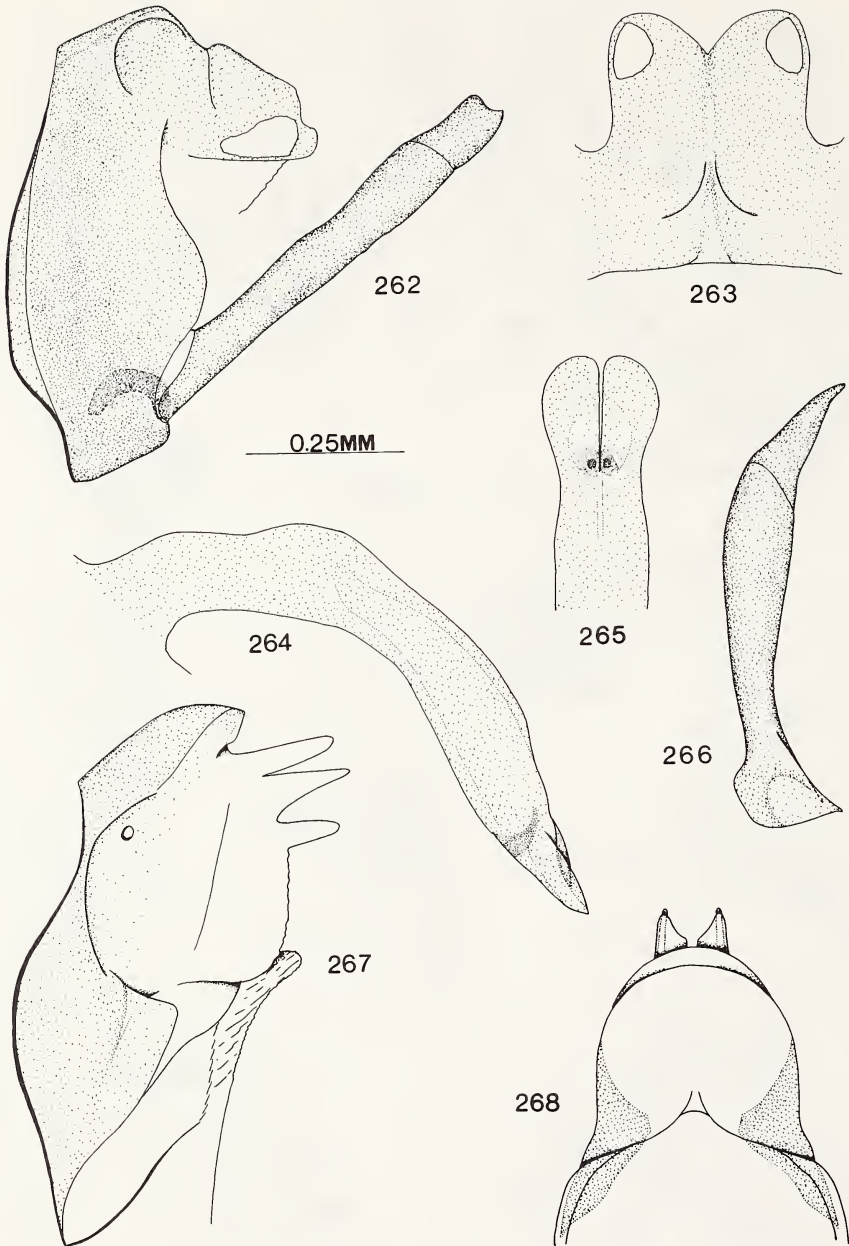
Fig. 262–268, *Hydropsyche placoda* Ross: 262, genital capsule of male, lateral aspect; 263, genital capsule of male, dorsal aspect; 264, aedeagus of male, lateral aspect; 265, aedeagus of male, dorsal aspect of tip; 266, left clasper of male, posterior aspect; 267, genital segments of female, lateral aspect; 268, genital segments of female, dorsal aspect.
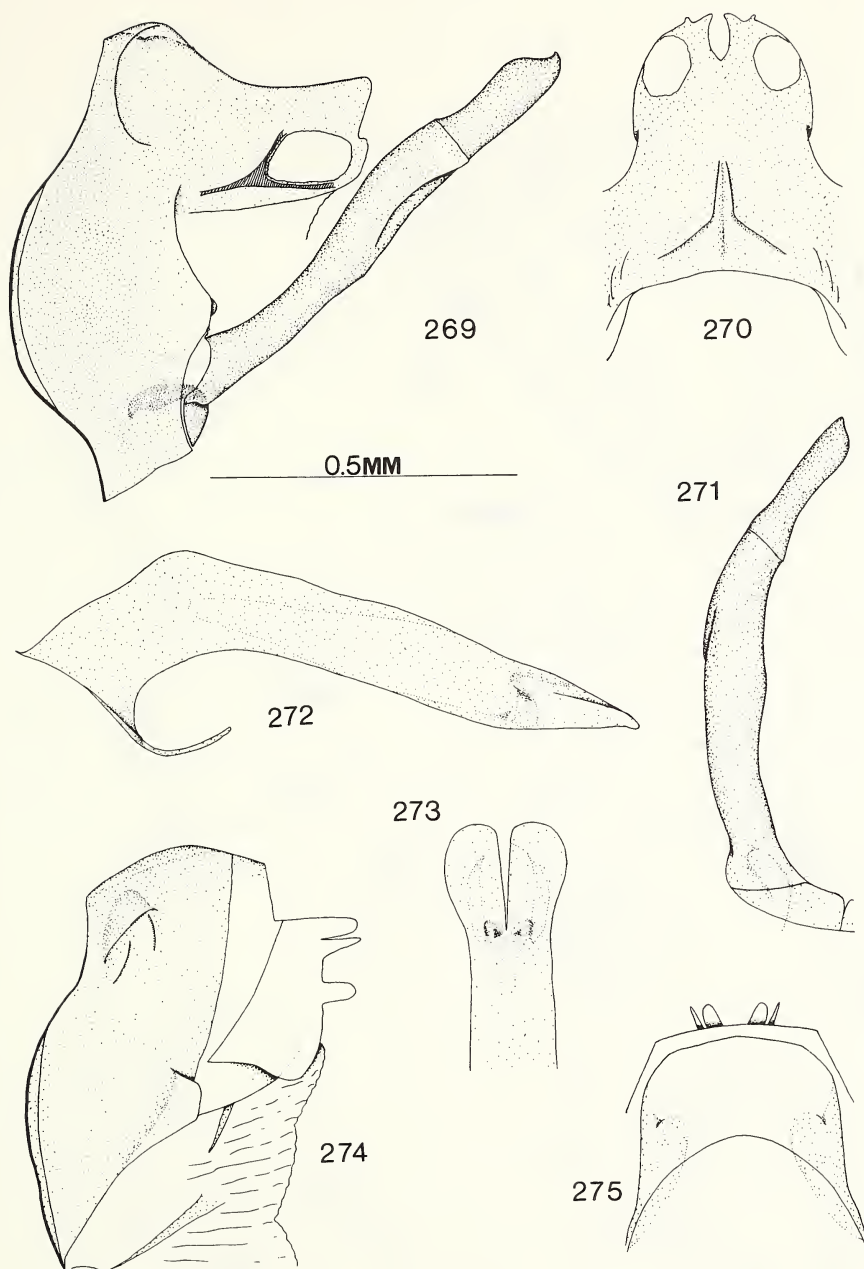
Fig. 269–275, *Hydropsyche rossi* Flint, Voshell, & Parker: 269, genital capsule of male, lateral aspect; 270, genital capsule of male, dorsal aspect; 271, left clasper of male, posterior aspect; 272, aedeagus of male, lateral aspect; 273, aedeagus of male, dorsal aspect of tip; 274, genital segments of female, lateral aspect; 275, genital segments of female, dorsal aspect.
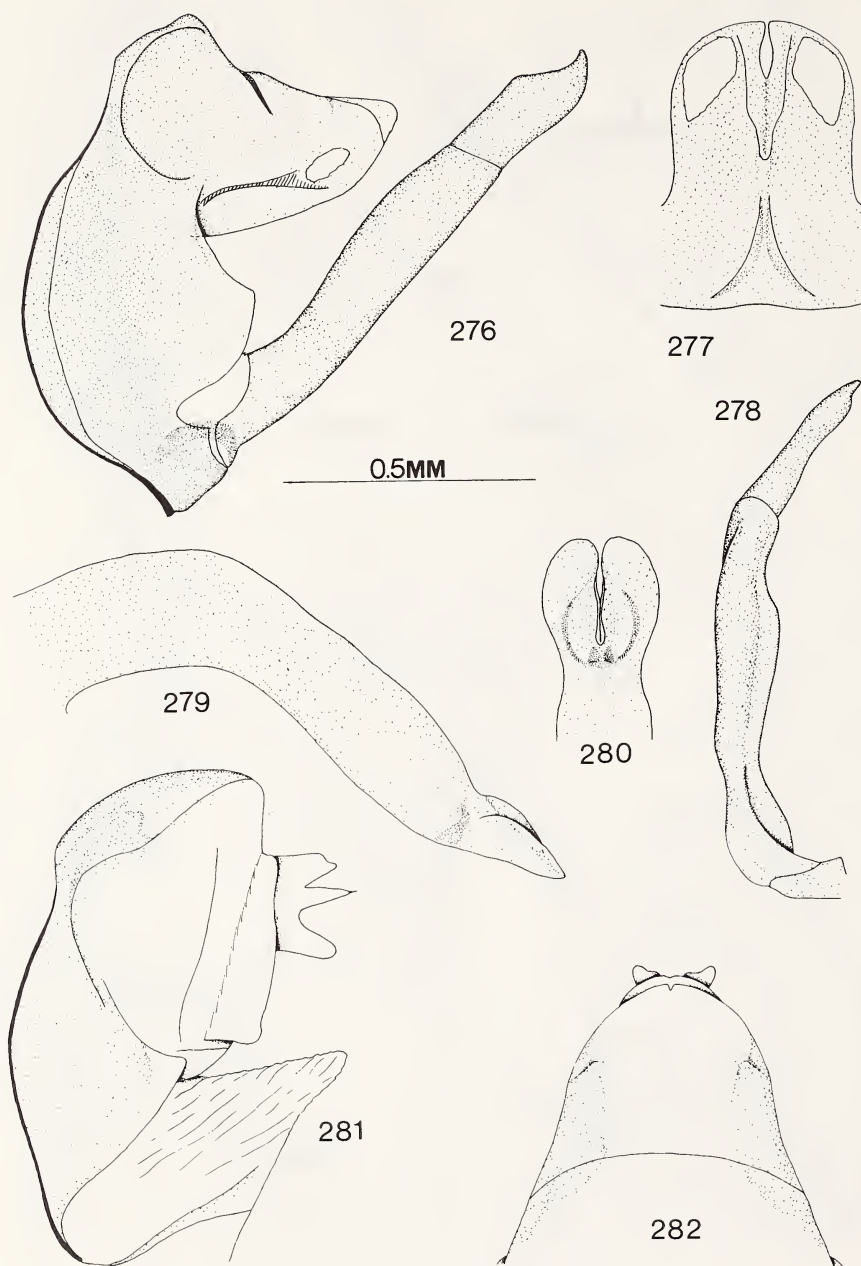
Fig. 276–282, *Hydropsyche scalaris* Hagen: 276, genital capsule of male, lateral aspect; 277, genital capsule of male, dorsal aspect; 278, left clasper of male, posterior aspect; 279, aedeagus of male, lateral aspect; 280, aedeagus of male, dorsal aspect of tip; 281, genital segments of female, lateral aspect; 282, genital segments of female, dorsal aspect.

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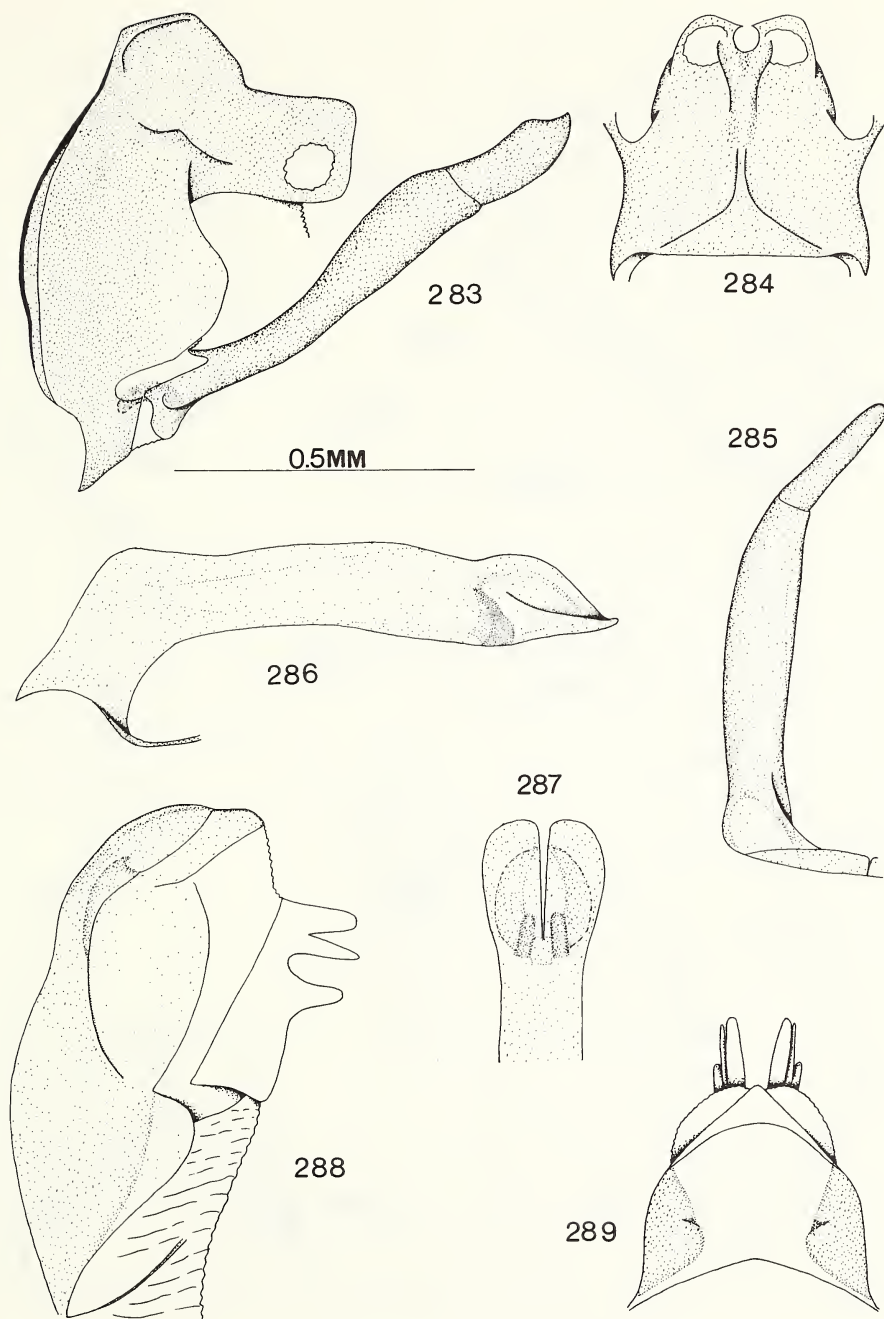
Fig. 283–289, *Hydropsyche simulans* Ross: 283, genital capsule of male, lateral aspect; 284, genital capsule of male, dorsal aspect; 285, left clasper of male, posterior aspect; 286, aedeagus of male, lateral aspect; 287, aedeagus of male, dorsal aspect of tip; 288, genital segments of female, lateral aspect; 289, genital segments of female, dorsal aspect.
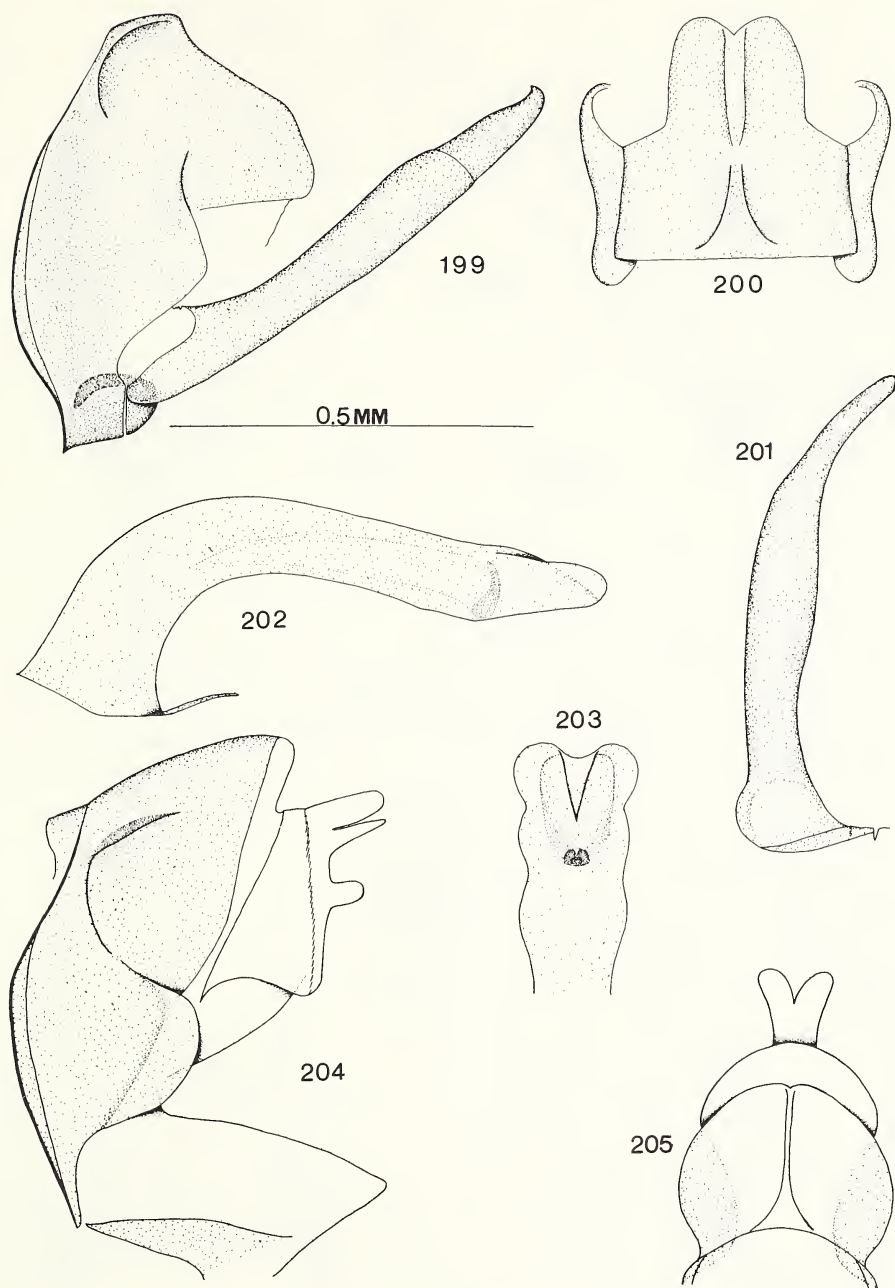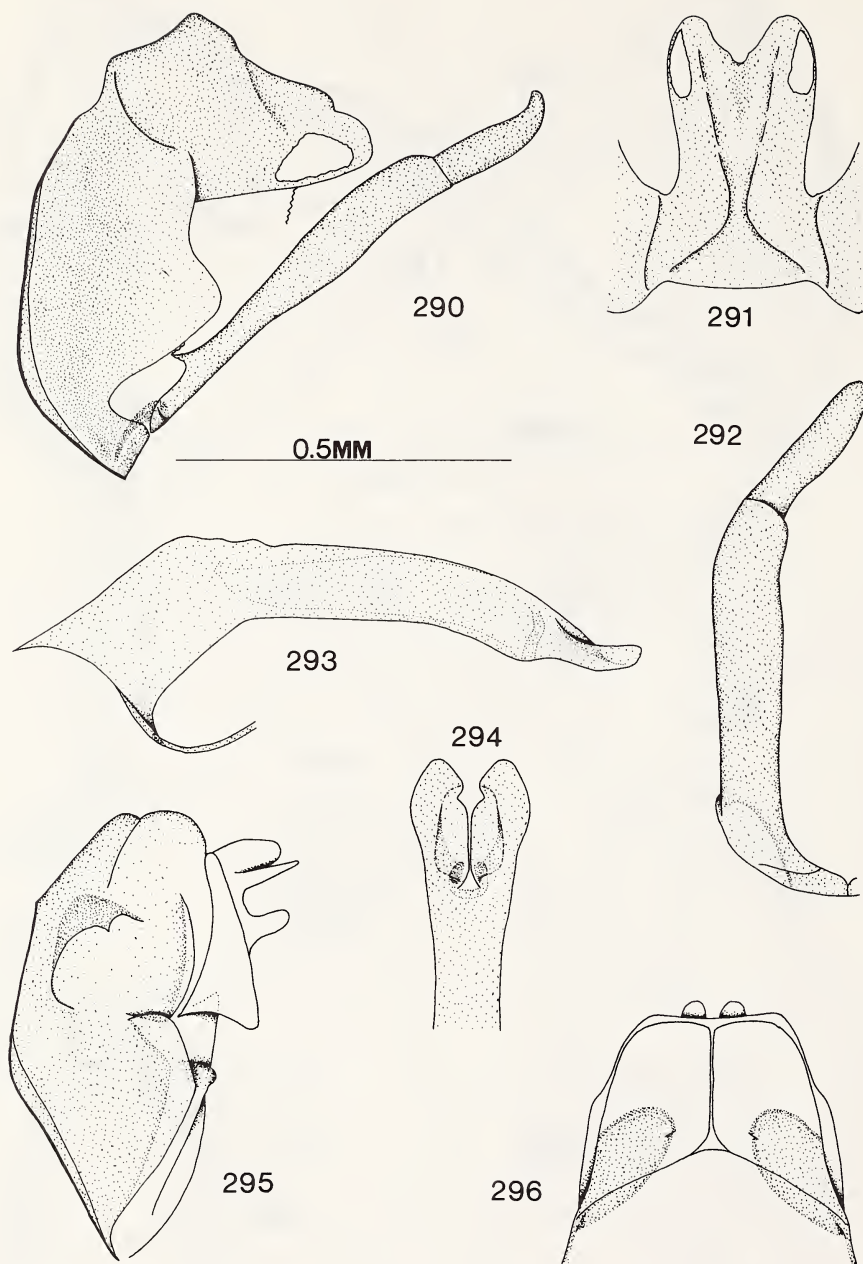
Fig. 290–296, *Hydropsyche valanis* Ross: 290, genital capsule of male, lateral aspect; 291, genital capsule of male, dorsal aspect; 292, left clasper of male, posterior aspect; 293, aedeagus of male, lateral aspect; 294, aedeagus of male, dorsal aspect of tip; 295, genital segments of female, lateral aspect; 296, genital segments of female, dorsal aspect.
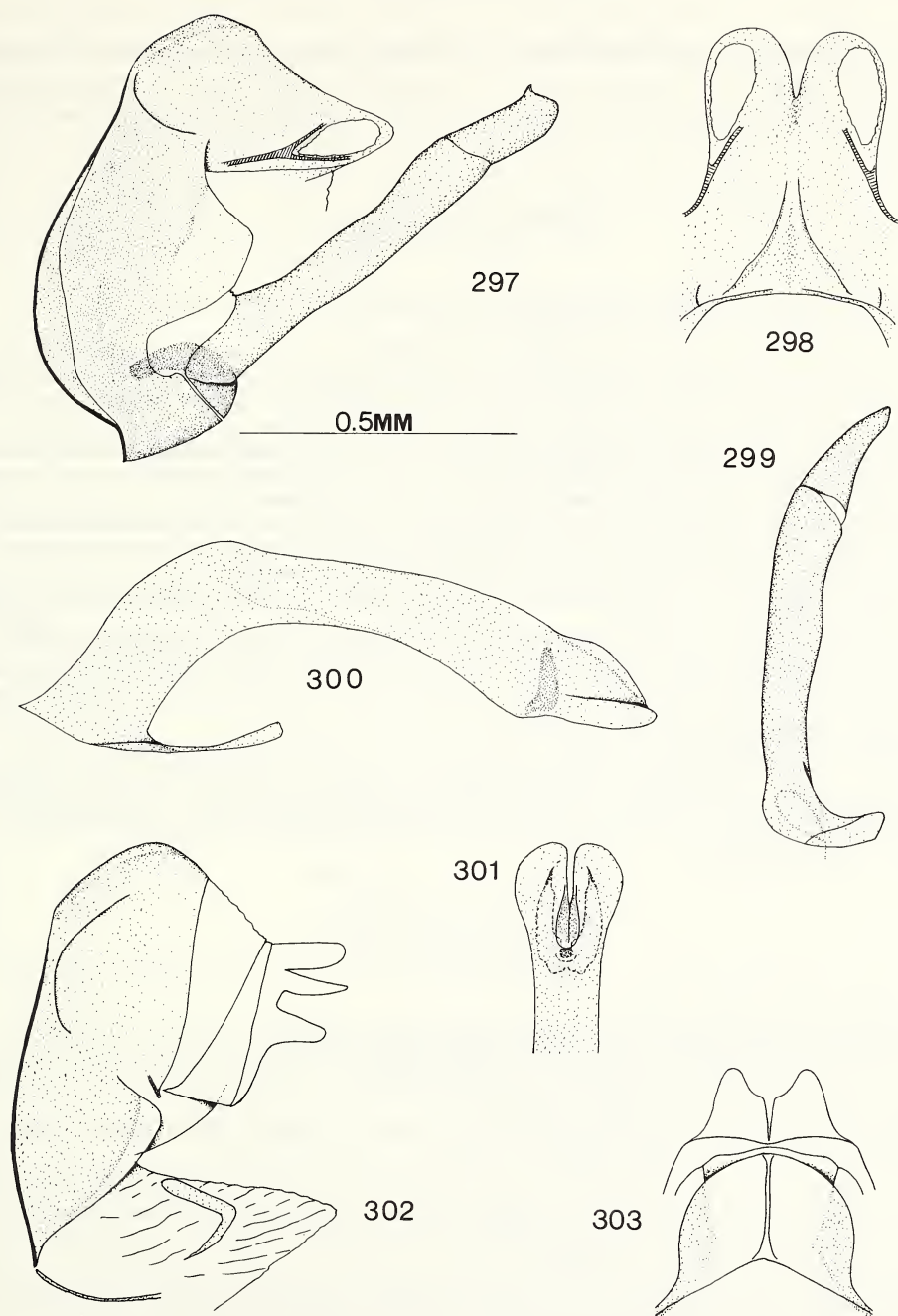
Fig. 297–303, *Hydropsyche venularis* Banks: 297, genital capsule of male, lateral aspect; 298, genital capsule of male, dorsal aspect; 299, left clasper of male, posterior aspect; 300, aedeagus of male, lateral aspect; 301, aedeagus of male, dorsal aspect of tip; 302, genital segments of female, lateral aspect; 303, genital segments of female, dorsal aspect.

SPECIES GROUP 2

This small group of species characterised by aedeagus sclerotised throughout, with distal end roughly, transversely truncate, of more or less uniform width throughout; and by clasper receptacle of females simple, blind invagination of lateral wall of segment X, without inner opening.

Hydropsyche betteni Ross
Map 49; Fig. 304–310

Hydropsyche betteni Ross, 1938b:146; Denning, 1943:122; Ross, 1944:99; Schuster & Etnier, 1978:61.
Hydropsyche incommoda not Hagen; Betten, 1934:188.

Description.— Male fore-wing length 10.53 mm; warm red-brown, with darker areas concentrated about Cu1 to A3. Hind-wing faintly tinted brown. Antennae red-brown; basal eight flagellar annuli each with oblique, dark band. Vertex yellow-brown. Spurs pale brown; lateral member of middle and hind-leg pairs shorter than mesal companions. Thorax deep, rich red-brown, to paler laterally. Legs brownish yellow; red-brown in female.

Genitalia. Male. (Fig. 304–308). (Specimen from St John's, Newfoundland). Males distinguished by aedeagus, in lateral aspect (Fig. 307), with base curved ventrad of remainder, in semi-circle; and by gap between distal lobes of tergum X, in dorsal aspect (Fig. 305), vase-shaped, each side of wider outer limit with distal tooth.

Genitalia. Female. (Fig. 309–310). (Specimen from St John's, Newfoundland). Females distinguished by clasper receptacle widened internally (Fig. 309), without inner opening (Fig. 310), with two lobes on floor of outer opening of receptacle; and by small, curved, slender secondary sclerotised strap laterally on vulval scale.

Biology.— Ross (1944) indicates that larvae prefer small to medium, riffled streams. They have been recorded in water film of dam spillways. Schuster & Etnier (1978) add that warmer waters are preferred; also, that this species is one of the more pollution-tolerant in *Hydropsyche*. It is, also, often the only *Hydropsyche* species in given streams. Canadian flight season extends from May 18 to October 2.

Distribution.— Recorded from Saskatchewan to Arkansas, Georgia, and Newfoundland, the species appears to be general throughout eastern North America, with extensions into the Boreal Forest (Map 49). In Canada it is recorded from Saskatchewan, then from northwestern Ontario to Newfoundland.

Hydropsyche confusa (Walker)
Map 50; Fig. 311–317

Philopotamus confusus Walker, 1852:103.
Hydropsyche confusa; Milne, 1936:61; Betten & Mosely, 1940:21; Nimmo, 1981:259.
Hydropsyche seperata Banks, 1936:129; Denning, 1943:121; Ross & Spencer, 1952:46 (as synonym of *H. guttata* Pictet); Smith, 1979:10; Nimmo, 1981:259 (as synonym of *H. confusa* (Walker)).
Hydropsyche guttata Pictet; Schuster & Etnier, 1978:126.
Hydropsyche corbetti Nimmo, 1966a:688; Schuster & Etnier, 1978:126 (as synonym of *H. guttata* Pictet); Nimmo, 1981:259 (as synonym of *H. confusa* (Walker)).

Description.— Male fore-wing length 8.66 mm; bright grey-brown, faintly irrorate; darker in female. Antennae brownish cream; basal nine flagellar annuli each with oblique, dark band. Vertex dark grey-brown. Spur formula 1,4,4 in male; 2,4,4 in female; pale brown; lateral member of middle leg pairs notably shorter than mesal companions. Thorax dark brown, to orange-brown laterally. Legs dull pale brown.

Genitalia. Male. (Fig. 311–315). (Specimen from Empress, Alberta). Males distinguished by distal article of clasper, in lateral aspect (Fig. 311), long, slightly bulbous distally, curved dorsad; by distal article, in posterior aspect (Fig. 313), hooked mesad; and by almost total lack of gap between distal lobes of tergum X, in dorsal aspect (Fig. 312).

Genitalia. Female. (Fig. 316–317). (Specimen from Empress, Alberta). Females distinguished by large, rounded clasper receptacle, in lateral aspect (Fig. 316), with two lobes on floor of receptacle entrance; and by presence of small, angled, secondary sclerotised strap on side of vulval scale.

Biology.— Smith (1979) presents a comprehensive account from Saskatchewan: univoltine, with extended emergence and flight season; pupae obtained from May 26 to August 24, with peak in June-July; larvae primarily detritovores and herbivores; appear to prefer larger, more turbid rivers.

Distribution.— Presently known from British Columbia and Washington to Québec in east, and Hudson's Bay and arctic coasts in north, this species is known in United States only from northern tier of States (Map 50). Canadian distribution records scattered; this species is recorded from nearly the southern-most point to Canadian Arctic Coast, though not north of tree line. Not known from eastern Québec or Atlantic Provinces.

Hydropsyche cuanis Ross
Map 51; Fig. 318–324

Hydropsyche cuanis Ross, 1938b:147; Ross, 1944:100; Schuster & Etnier, 1978:70.

Description.— Male fore-wing length 9.36 mm; light orange-brown, with no evident markings. Hind-wing faintly tinted. Antennae yellow; basal eight flagellar annuli each with oblique, dark band (five in female). Vertex deep reddish brown, narrowed anterad, with compound eyes of male much larger, relatively, than in most other species; female normal. Spurs yellow; lateral member of middle and hind-leg pairs notably shorter than mesal companions; applicable in the female to middle leg pairs only. Thorax rich red-brown, to more orange-brown laterally. Legs pale orange-brown to straw.

Genitalia. Male. (Fig. 318–322). (Specimen from Momence, Illinois, USA). Males distinguished by basal article of clasper narrow at base, widened distally, in lateral aspect (Fig. 318); by uniform width of basal article, in posterior aspect (Fig. 320); by distal article narrowed in two stages, to acuminate tip (Fig. 318); and by gap between tergum X distal lobes v-shaped.

Genitalia. Female. (Fig. 323–324). (Specimen from Kankakee R., Willmington, Illinois, USA – Paratype). Females distinguished by sclerotised strap of vulval scale narrow, sinuate (Fig. 323); by clasper receptacle relatively narrow, rounded, directed dorso-anterad, without grooves or lobes on receptacle floor (Fig. 323); and by receptacle without inner opening (Fig. 324).

Biology.— Ross (1944) indicates that larvae prefer swift rapids areas of larger rivers. Flight season apparently commences with May peak, which declines into August.

Distribution.— Limited to mid-west States of USA (Map 51). Not yet known from Canada.

Hydropsyche depravata Hagen
Map 52; Fig. 325–331

Hydropsyche depravata Hagen, 1861:290; Betten, 1934:187; Milne, 1036:70, 72, 73; Ross, 1944:100; Schuster & Etnier, 1978:63.

Description.— Male fore-wing length 9.75 mm; grey-brown, uniformly irrorate. Hind-wing very faintly tinted grey-brown. A tennae red-brown; basal nine flagellar annuli each with oblique, dark band – eight in female. Vertex dark brown. Spurs brown – yellow in female; lateral member of all pairs shorter than mesal companions. Thorax dark brown, to red-brown laterally. Legs straw-coloured.

Genitalia. Male. (Fig. 325–329). (Specimen from Beaver Ck, Knox Co., Tennessee, USA). Males distinguished by distal article of clasper, in lateral aspect (Fig. 325), evenly tapered from base to rounded tip (tip curved abruptly); by pair of black sclerites housed in tip of aedeagus, as seen in dorsal aspect (Fig. 329); and by gap between tergum X distal lobes wide, v-shaped, not deep (Fig. 326).

Genitalia. Female. (Fig. 330–331). (Specimen from Beaver Ck, Knox Co., Tennessee, USA). Females distinguished by clasper receptacle large, rounded, with pair of grooves on floor of receptacle opening, without inner opening (Fig. 330, 331); and by only dorsal lobes of segment XI visible in dorsal aspect.

Biology.— Schuster & Etnier (1978) state that larvae live in warm-water, small streams with high organic loading. Apparently found mostly on medium-sized rocks in riffles. Only flight record available is for July 26, in Saskatchewan.

Distribution.— Primarily known from Indiana to Georgia to Virginia, with isolated record from prairie of southern Saskatchewan, in Canada (Map 52).

Map 49. Collection localities for *Hydropsyche betteni* Ross in Canada, with known distribution in North America by state or province.
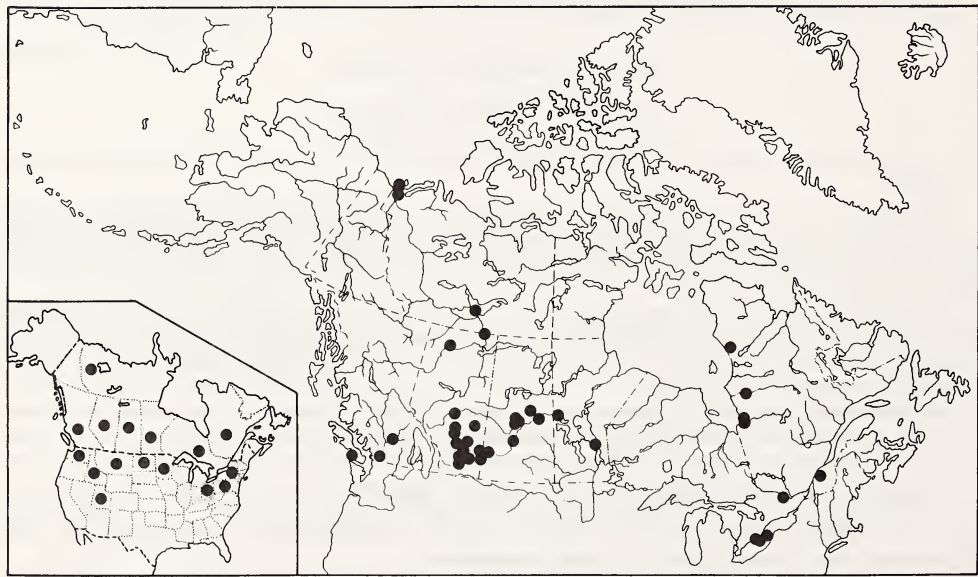
Map 50. Collection localities for *Hydropsyche confusa* (Walker) in Canada, with known distribution in North America by state or province.
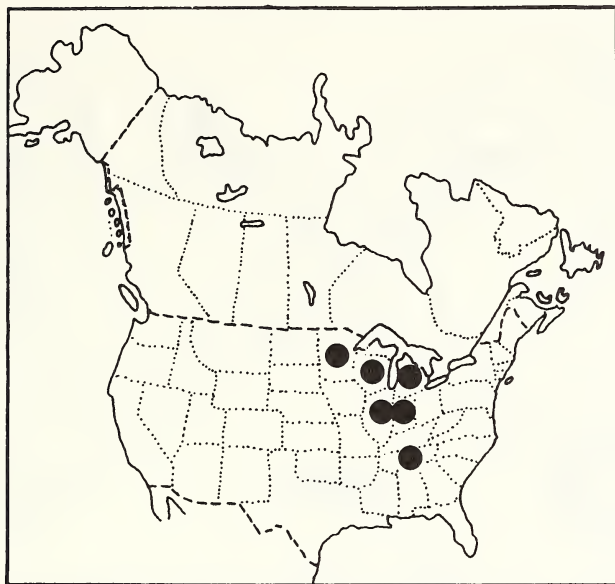
Map 51. Known distribution of *Hydropsyche cuanis* Ross in North America, by state.

Map 52. Collection localities for *Hydropsyche depravata* Hagen in Canada, with known distribution in North America by state or province.

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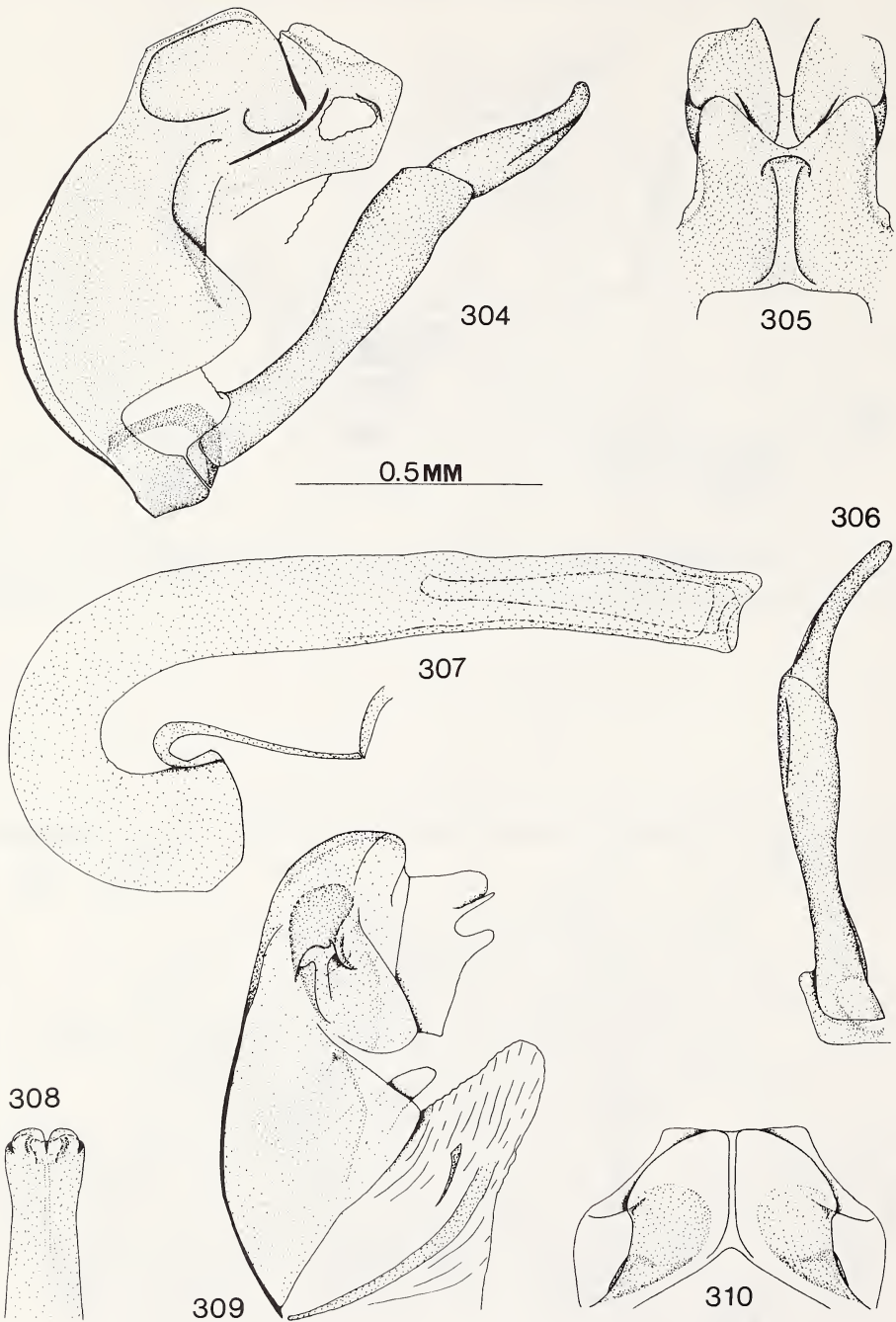
Fig. 304–310, *Hydropsyche betteni* Ross: 304, genital capsule of male, lateral aspect; 305, genital capsule of male, dorsal aspect; 306, left clasper of male, posterior aspect; 307, aedeagus of male, lateral aspect; 308, aedeagus of male, dorsal aspect of tip; 309, genital segments of female, lateral aspect; 310, genital segments of female, dorsal aspect.

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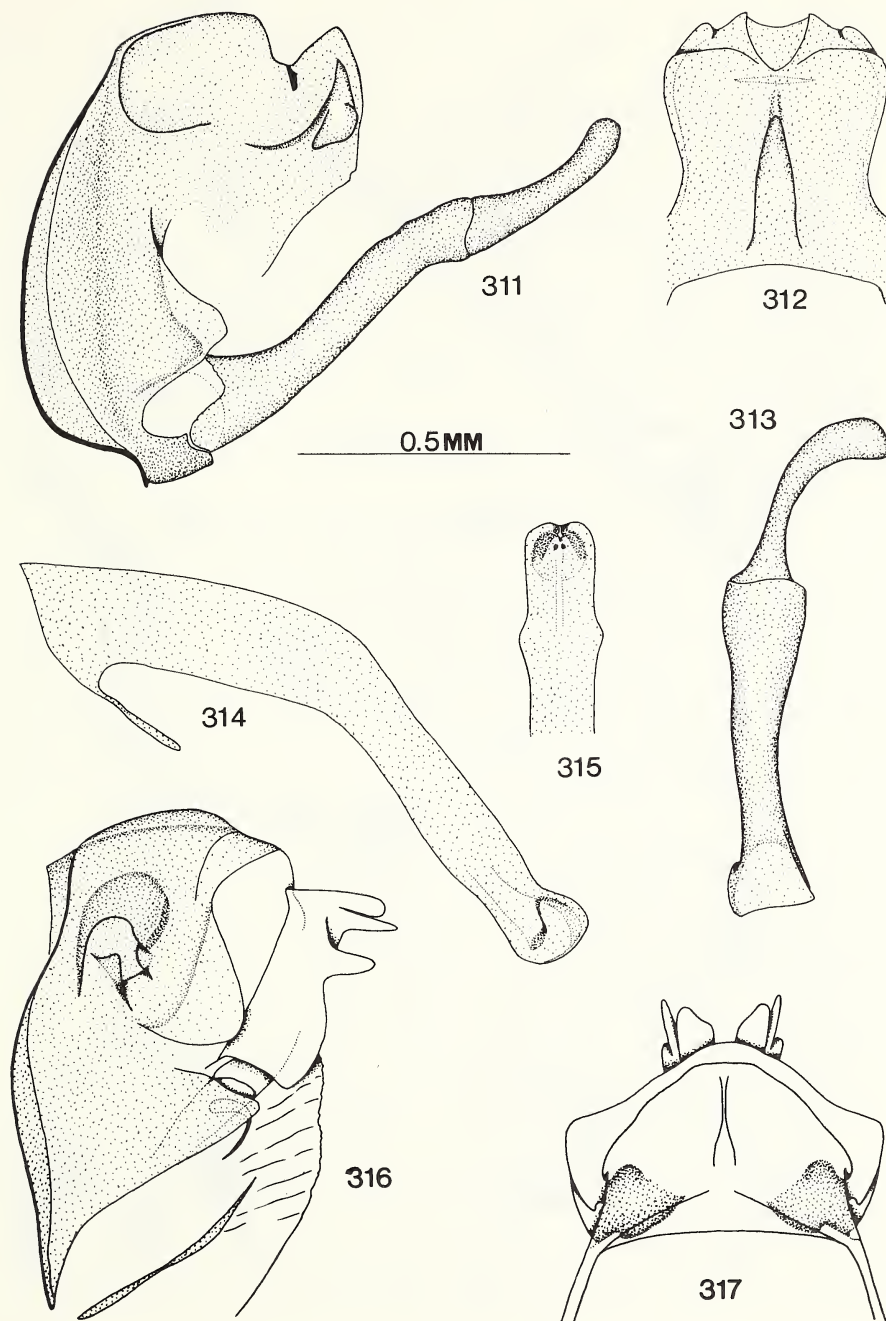
Fig. 311–317, *Hydropsyche confusa* (Walker): 311, genital capsule of male, lateral aspect; 312, genital capsule of male, dorsal aspect; 313, left clasper of male, posterior aspect; 314, aedeagus of male, lateral aspect; 315, aedeagus of male, dorsal aspect of tip; 316, genital segments of female, lateral aspect; 317, genital segments of female, dorsal aspect.
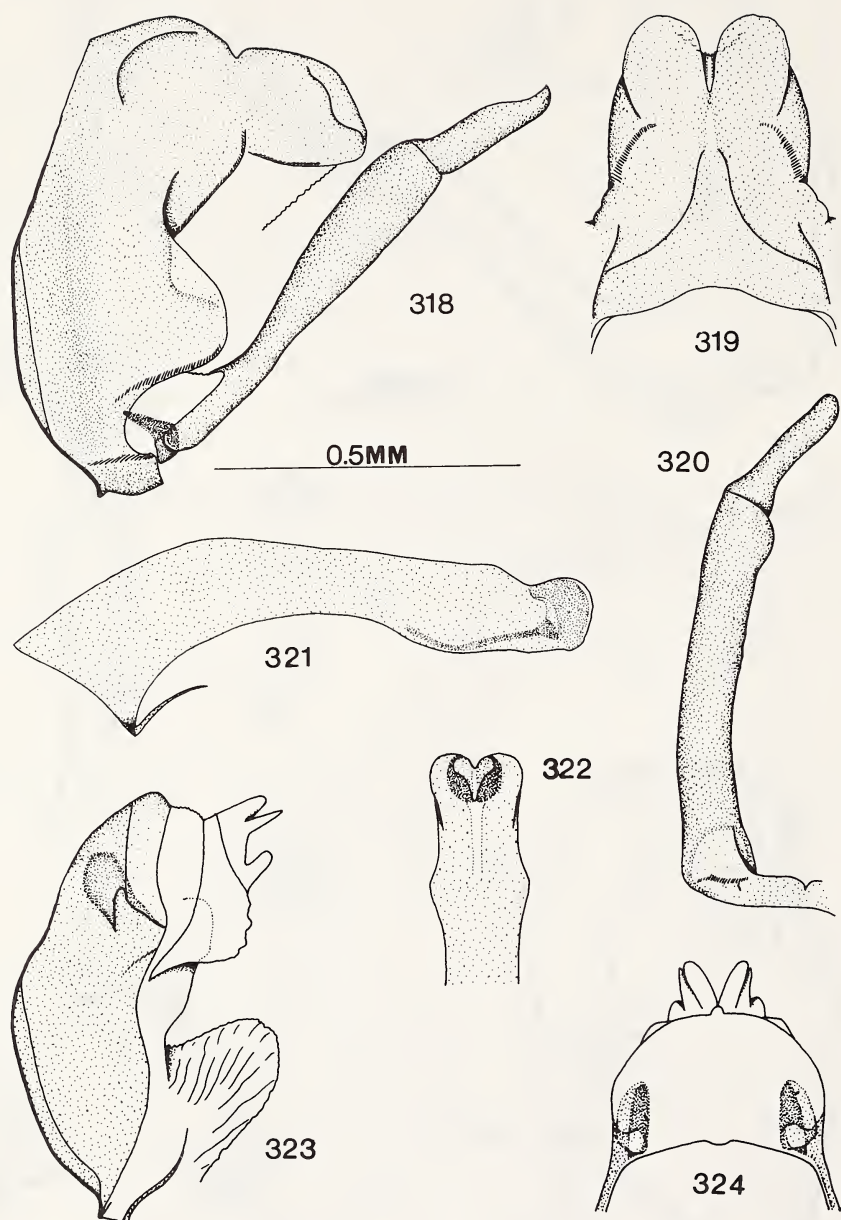
Fig. 318–324, *Hydropsyche cuanis* Ross: 318, genital capsule of male, lateral aspect; 319, genital capsule of male, dorsal aspect; 320, left clasper of male, posterior aspect; 321, aedeagus of male, lateral aspect; 322, aedeagus of male, dorsal aspect of tip; 323, genital segments of female, lateral aspect; 324, genital segments of female, dorsal aspect.

0.5MM
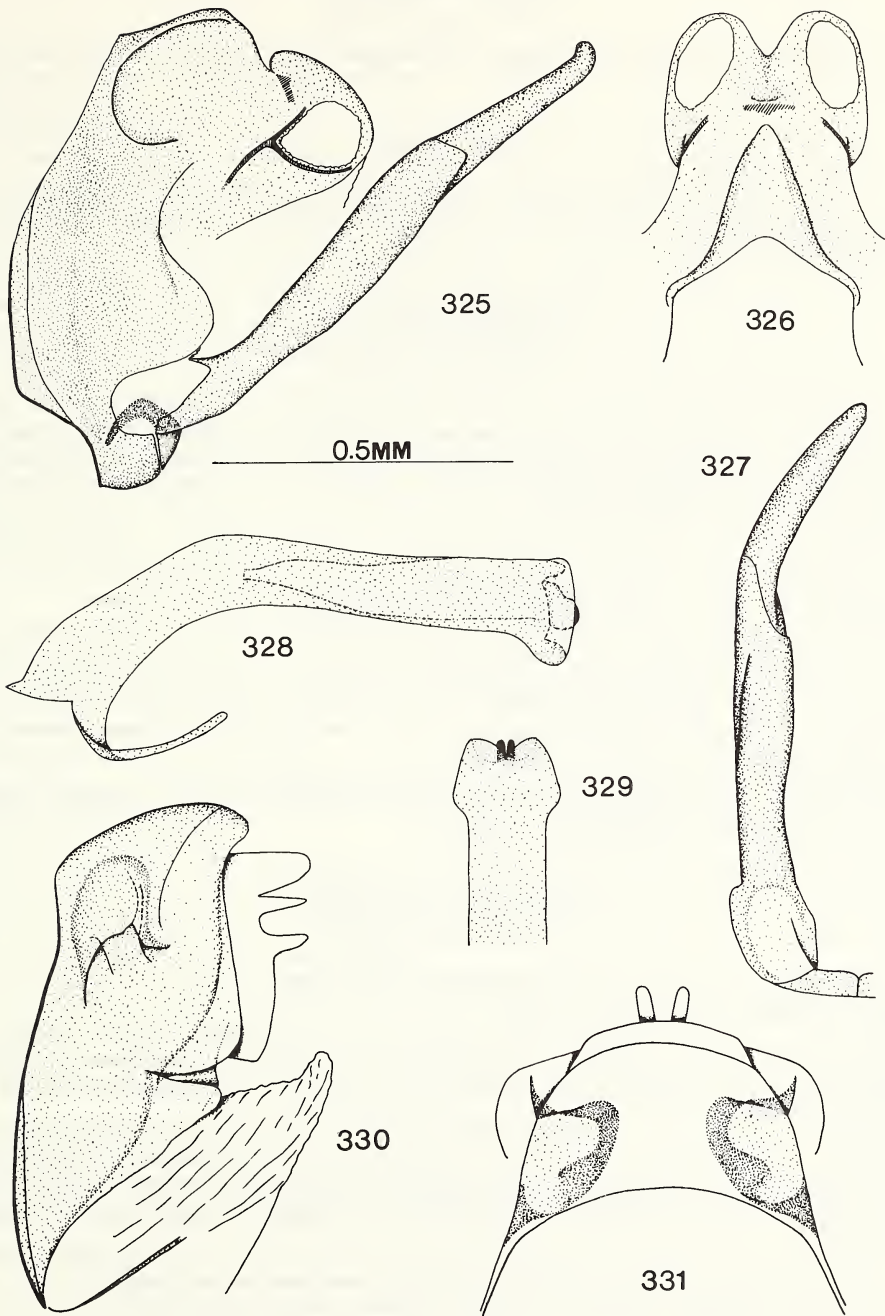
Fig. 325–331, *Hydropsyche depravata* Hagen: 325, genital capsule of male, lateral aspect; 326, genital capsule of male, dorsal aspect; 327, left clasper of male, posterior aspect; 328, aedeagus of male, lateral aspect; 329, aedeagus of male, dorsal aspect of tip; 330, genital segments of female, lateral aspect; 331, genital segments of female, dorsal aspect.

SPECIES GROUP 3

This group characterised by aedeagus with toothed and/or spinate membranous lobes distally.

SUBGROUP A

This subgroup characterised by possession of membranous lobes on aedeagus both dorsally and ventro-laterally.

Hydropsyche amblis Ross
Map 53; Fig. 332–338

Hydropsyche amblis Ross, 1938a:120; Ross, 1944:294; Anderson, 1976:65; Schefter & Wiggins, 1986:51.

Description.— Male fore-wing length 9.13 mm; pale cream-brown, with hint of irroration around distal edge. Hind-wing hyaline. Antennae red-brown; no oblique dark bands. Vertex dark brown, warts cream. Spurs straw-coloured; lateral member of middle leg pairs, and hind-leg apical pair, notably shorter than mesal companions. Thorax deep red-brown, to paler laterally. Legs straw coloured.

Genitalia. Male. (Fig. 332–336). (Specimen from East Fork, Humbug Ck, Clatsop Co., Oregon, USA). Males distinguished by massive, postero-ventrally directed distal lobes of tergum X, in lateral aspect (Fig. 332); by tooth of dorsal lobe of aedeagus directed postero-dorsad (Fig. 335); by ventro-lateral lobes of aedeagus directed antero-ventrad, with bundle of spines at tip; and by tip of distal article of clasper, in lateral aspect, with small curved indentation.

Genitalia. Female. (Fig. 337–338). (Specimen from Okop Ck, Eatonville, Washington, USA). Females distinguished by small, anteriorly directed clasper receptacle traversed by thin, dark line which passes down lateral wall of segment X; by small, irregular sclerotised strap of vulval scale (Fig. 337); and by clasper receptacle, in dorsal aspect (Fig. 338), directed antero-mesad, without visible inner openings.

Biology.— Anderson (1976) suggests that larvae prefer small streams. Emergence has been recorded from early May to mid-August in Oregon.

Distribution.— Presently known only from Lower Mainland of British Columbia, Canada and from Washington and Oregon, USA (Map 53).

Hydropsyche piatrix Ross
Map 54; Fig. 339–345

Hydropsyche piatrix Ross, 1938b:148; Ross, 1944:97; Schefter & Wiggins, 1986:68.
Symphitopsyche piatrix; Schuster & Etnier, 1978:57.

Description.— Male fore-wing length 7.84 mm; uniform yellowish brown, very faintly irrorate. Hind-wing paler. Antennae pale yellowish brown, no oblique, dark bands. Vertex brown, warts paler. Spurs brownish straw; lateral member of middle leg pairs notably shorter than mesal companions. Thorax dark brown, to grey-brown laterally. Legs pale brownish straw, to straw.

Genitalia. Male. (Fig. 339–343). (Specimen from Mammoth Springs, Arkansas, USA – Paratype). Males distinguished by tergum X distal lobes small, rounded, curved slightly ventrad in lateral aspect (Fig. 339); by these lobes, in dorsal aspect, finger-like, curved postero-mesad, gap between elliptical; by ventro-lateral lobe of aedeagus tapered anterad, without teeth or spines (Fig. 342); and by dorsal lobe not produced, with minute tooth directed slightly antero-laterad.

Genitalia. Female. (Fig. 344–345). (Specimen from Mammoth Springs, Arkansas, USA). Females distinguished by clasper receptacle directed dorso-posterad in lateral aspect (Fig. 344), meso-posterad in dorsal aspect (Fig. 345); by vulval scale with two sclerotised straps in lateral aspect – primary club-shaped, secondary triangular, dorsal; and by segment XI dorsal lobe, in dorsal aspect (Fig. 345) large enough to obscure all beneath, with mesal shoulder.

Biology.— Very little known except that this species has been taken only at spring-like waters (Schuster & Etnier, 1978). Only flight dates available are from June and early July.

Distribution.— Very scattered – North Dakota, Missouri, Arkansas, and St Lawrence R. valley of Québec (Map 54).

Hydropsyche vexa Ross
Map 55; Fig. 346–352

Hydropsyche vexa Ross, 1938b:148; Denning, 1943:124; Ross, 1944:97; Schefter & Wiggins, 1986:81.
Symphitopsyche vexa; Schuster & Etnier, 1978:127.

Description.— Male fore-wing length 7.41 mm; golden brown, faintly irrorate. Antennae pale brown; basal seven or eight flagellar annuli each with oblique, dark band; five in female, paler. Vertex orange-brown. Spurs yellow; lateral member of middle leg pairs, and hind-leg apical pair, notably shorter than mesal companions; applies only to middle leg pairs in female. Thorax orange-brown, to yellow-brown laterally. Legs pale brownish yellow.

Genitalia. Male. (Fig. 346–350). (Specimen from White Earth R., Hwy 28, Alberta). Males distinguished by basal article of clasper, in lateral aspect (Fig. 346), with slender base, expanded distally; by tergum X distal lobes long, thin, curved slightly ventrad in lateral aspect (Fig. 346), curved mesad in dorsal aspect (Fig. 347), space between almost enclosed; by dorsal membranous lobe of aedeagus small, with small, acuminate tooth directed posterad (Fig. 349, 350); and by ventro-lateral lobe of aedeagus long, straight, directed antero-ventrad, with distal pocket of spines.

Genitalia. Female. (Fig. 351–352). (Specimen from White Earth R., Hwy 28, Alberta). Females distinguished by clasper receptacle, in lateral aspect (Fig. 351), directed dorsad, of medium size, with two grooves on floor at entrance; and by clasper receptacle, in dorsal aspect (Fig. 352), curved postero-mesad.

Biology.— Very little known. Flight records extend from May 22 to August 8 in Canada.

Distribution.— Recorded in narrow zone across Continent, from Idaho and Alberta to New Brunswick and Maine (Map 55). In Canada known only from Prairie Provinces, Montréal, and New Brunswick.

Hydropsyche walkeri Betten & Mosely
Map 56; Fig. 353–359

Hydropsyche maculicornis Walker, 1852:113 (preoccupied by Pictet, 1834 – now in *Tinodes*).
Hydropsyche walkeri Betten & Mosely, 1940:23 (new name); Ross, 1944:96; Schefter & Wiggins, 1986:83.
Symphitopsyche walkeri; Schuster & Etnier, 1978:35.

Description.— Male fore-wing length 7.53 mm; pale red-brown. Hind-wing very palely tinted yellow-brown. Antennae uniformly brown. Vertex dark reddish brown, warts paler. Spurs yellow-brown; lateral member of fore-leg apical pair much finer than mesal companion, hyaline. Thorax dark reddish brown, to grey-brown laterally. Legs yellowish brown. Warts, generally, paler.

Genitalia. Male. (Fig. 353–357). (Specimen from St Hippolyte, Québec). Males distinguished by distal article of clasper with distal half bent dorsad at approximately 45° to basal half, with tip slightly scalloped (Fig. 353); by tergum X distal lobes with dorsal edge angled in lateral aspect (Fig. 353), lobes curved mesad, in dorsal aspect (Fig. 354), space between almost enclosed; by aedeagus with ventro-lateral lobe directed basad along side (Fig. 356); and by dorsal lobes of aedeagus slightly developed, tooth directed postero-dorsad.

Genitalia. Female. (Fig. 358–359). (Specimen from St Hippolyte, Québec). Females distinguished by large, crescent-shaped clasper receptacle located in postero-dorsal angle of segment X (Fig. 358); and by sclerotised strap of vulval scale large, long, wide except tapered basad.

Biology.— According to Schuster & Etnier (1978) larvae appear to prefer small to medium sized streams with coarse gravel to small rock bottom, which are rich in organic materials. Riffle areas appear to be preferred, with smoothly-flowing water. Canadian flight season extends from May 5 to September 2.

Distribution.— From Saskatchewan to Virginia, Maine, and Québec (Map 56). In Canada recorded from northcentral Saskatchewan to east coast of Hudson's Bay, south to southern Québec and Ontario.

Map 53. Collection localities for *Hydropsyche amblis* Ross in Canada, with known distribution in North America by state or province.
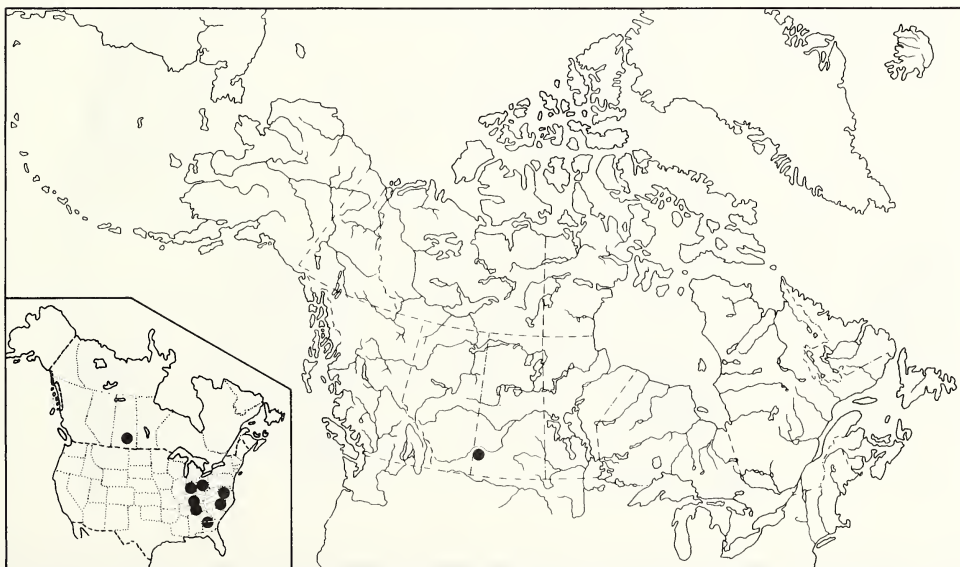

Map 54. Collection localities for *Hydropsyche piatrix* Ross in Canada, with known distribution in North America by state or province.
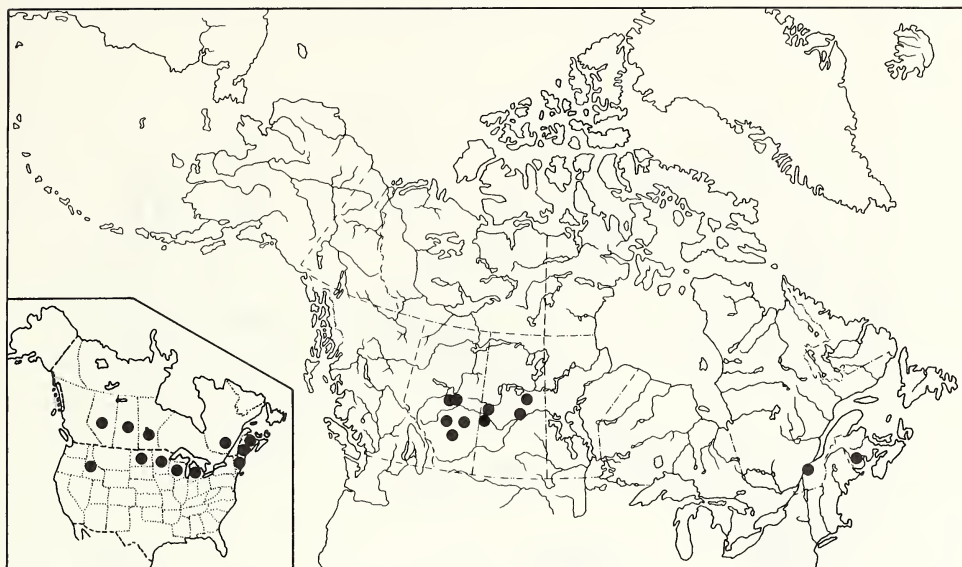
Map 55. Collection localities for *Hydropsyche vexa* Ross in Canada, with known distribution in North America by state or province.
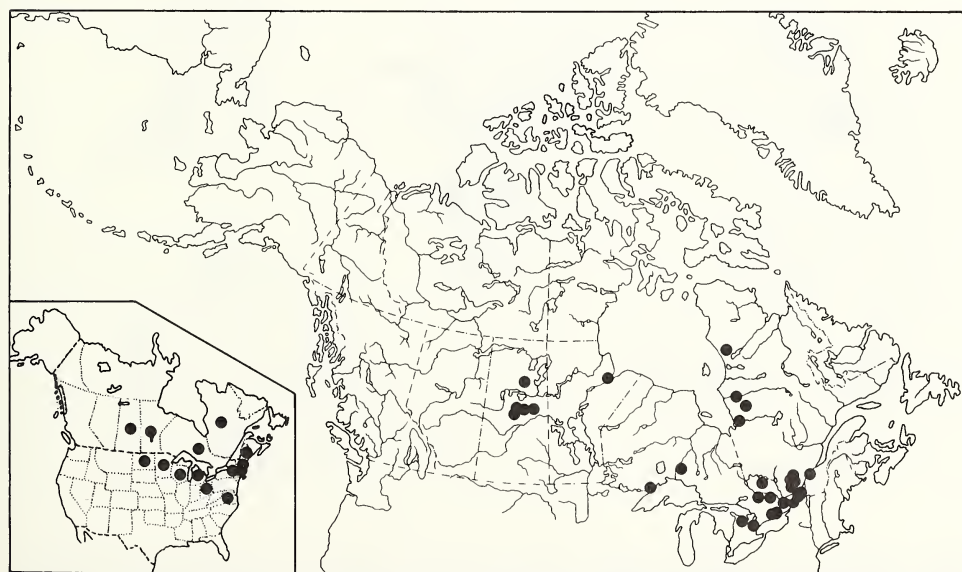
Map 56. Collection localities for *Hydropsyche walkeri* Betten & Mosely in Canada, with known distribution in North America by state or province.
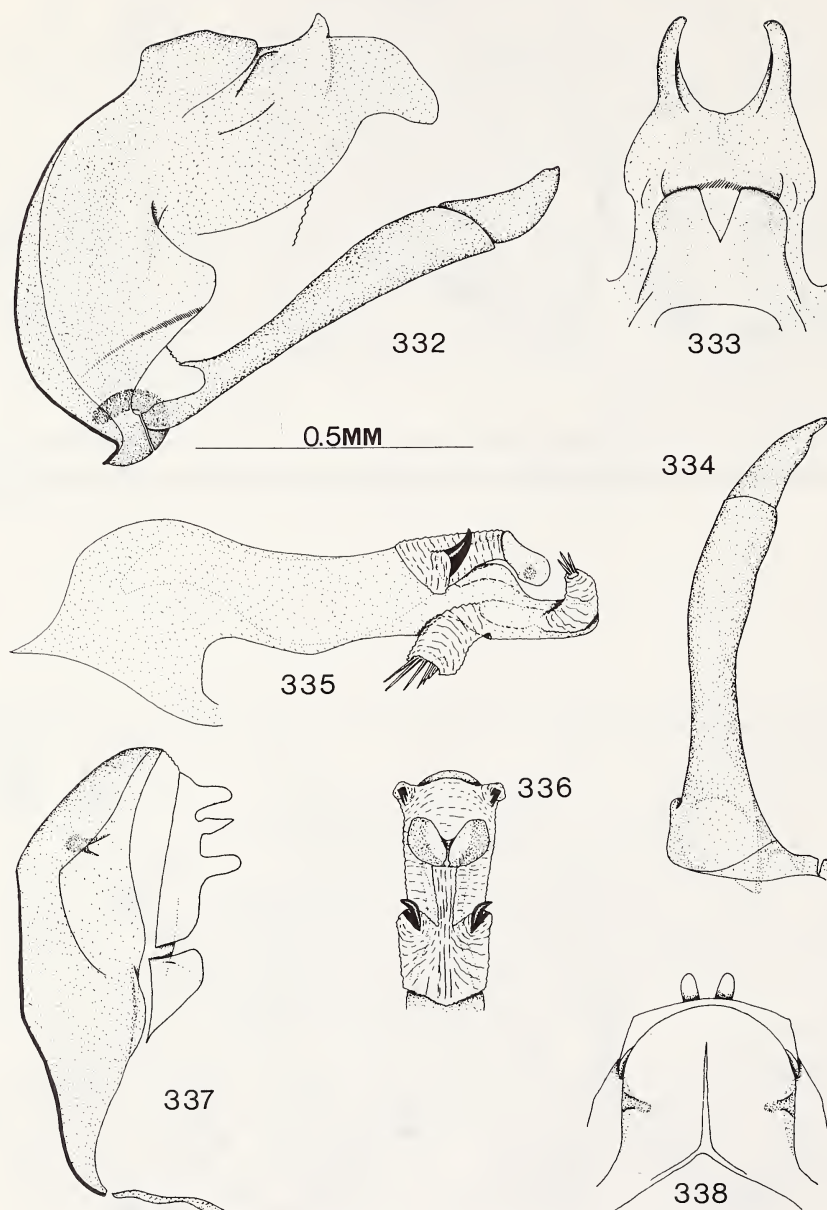
Fig. 332–338, *Hydropsyche amblis* Ross: 332, genital capsule of male, lateral aspect; 333, genital capsule of male, dorsal aspect; 334, left clasper of male, posterior aspect; 335, aedeagus of male, lateral aspect; 336, aedeagus of male, dorsal aspect of tip; 337, genital segments of female, lateral aspect; 338, genital segments of female, dorsal aspect.
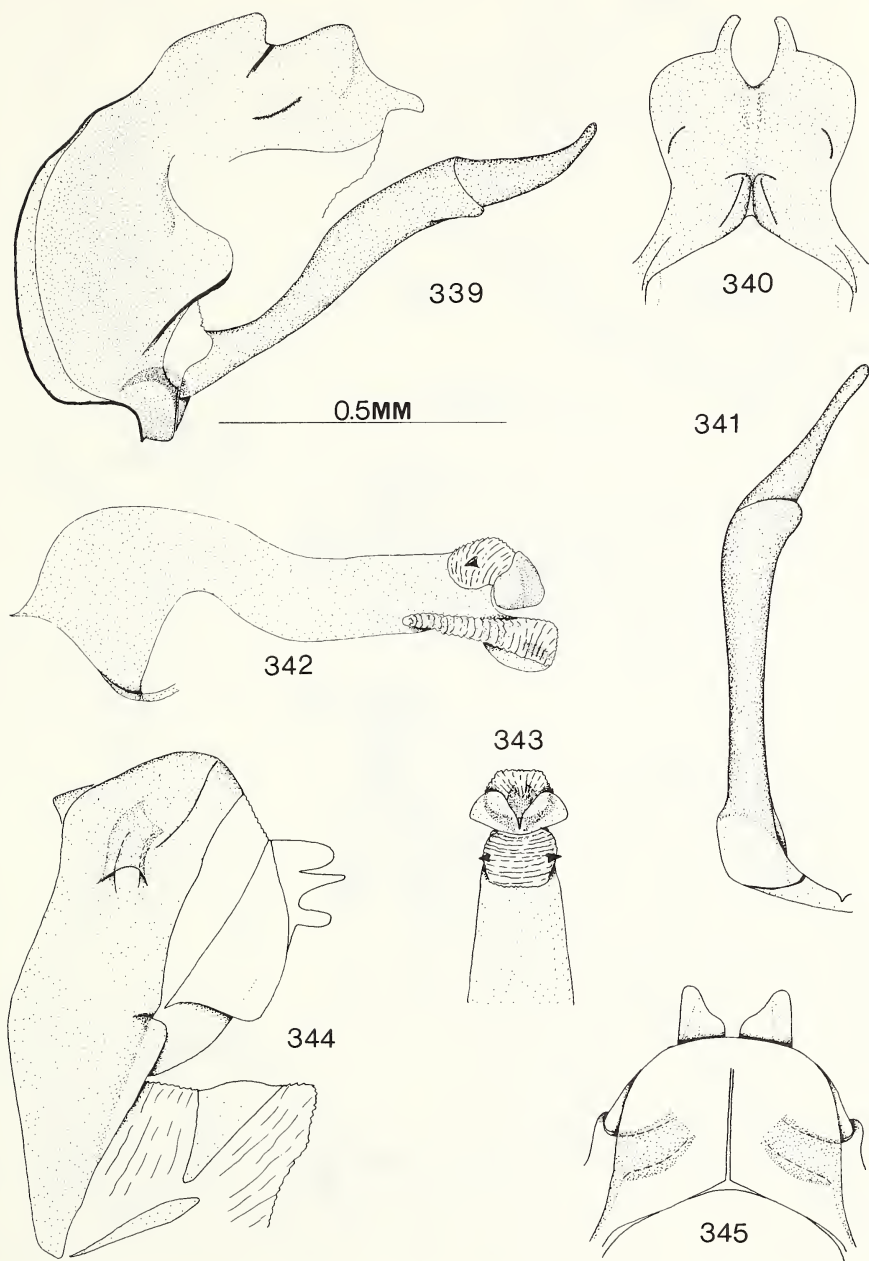
Fig. 339–345, *Hydropsyche piatrix* Ross: 339, genital capsule of male, lateral aspect; 340, genital capsule of male, dorsal aspect; 341, left clasper of male, posterior aspect; 342, aedeagus of male, lateral aspect; 343, aedeagus of male, dorsal aspect of tip; 344, genital segments of female, lateral aspect; 345, genital segments of female, dorsal aspect.
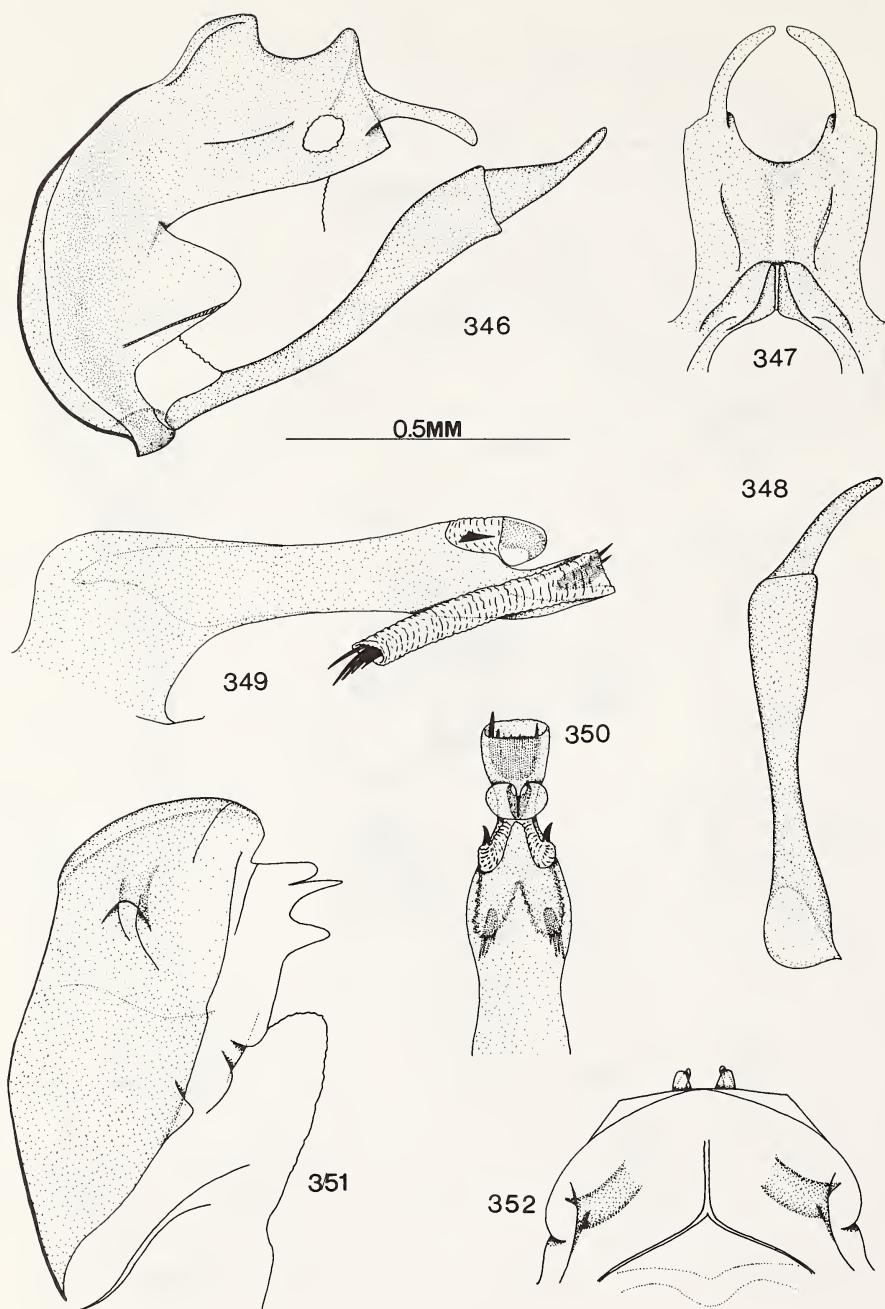
Fig. 346–352, *Hydropsyche vexa* Ross: 346, genital capsule of male, lateral aspect; 347, genital capsule of male, dorsal aspect; 348, left clasper of male, posterior aspect; 349, aedeagus of male, lateral aspect; 350, aedeagus of male, dorsal aspect of tip; 351, genital segments of female, lateral aspect; 352, genital segments of female, dorsal aspect.

0.5MM
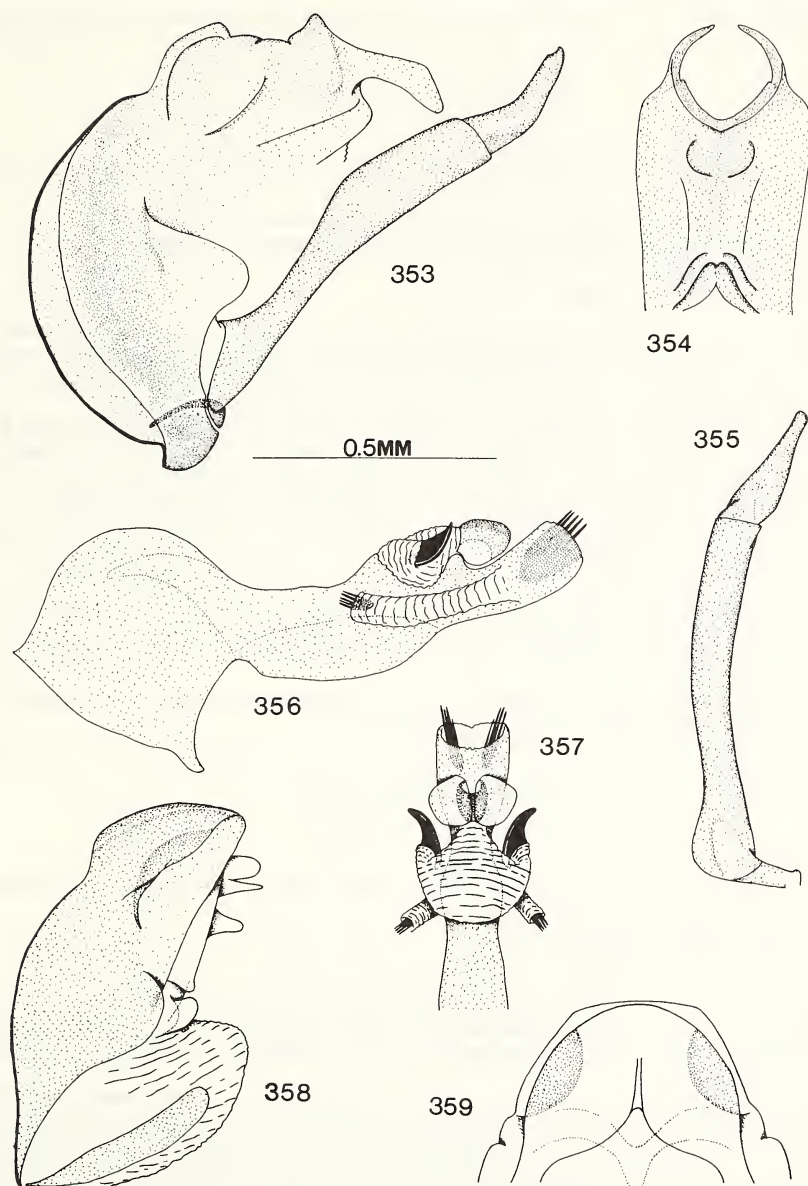
Fig. 353–359, *Hydropsyche walkeri* Betten & Mosely: 353, genital capsule of male, lateral aspect; 354, genital capsule of male, dorsal aspect; 355, left clasper of male, posterior aspect; 356, aedeagus of male, lateral aspect; 357, aedeagus of male, dorsal aspect of tip; 358, genital segments of female, lateral aspect; 359, genital segments of female, dorsal aspect.

SUBGROUP B

This subgroup characterised by aedeagus without ventro-lateral membranous lobes; distal tooth directed ventrad.

Hydropsyche alhedra Ross
Map 57; Fig. 360–366

Hydropsyche alhedra Ross, 1939:67; Ross, 1944:294; Schefter, Wiggins, & Unzicker, 1986:69; Schefter & Wiggins, 1986:45.
Hydropsyche riola Denning; Schefter, Wiggins, & Unzicker, 1986:69 (as synonym of *H. alhedra*).
Hydropsyche racona Denning; Schefter, Wiggins, & Unzicker, 1986:69 (as synonym of *H. alhedra*).
Symphitopsyche alhedra; Schuster & Etnier, 1978:45.

See note at end of 'Introduction'.

Description.— Male fore-wing length 9.09 mm; pale grey-brown, faintly irrorate posterad of M; female paler. Hind-wing hyaline. Antennae brown; basal seven flagellar annuli each with oblique, dark band; female paler. Vertex dark red-brown, warts paler; female paler. Spurs straw-coloured; mesal member of middle leg apical pair shorter than lateral companion. Thorax dark red-brown, to slightly paler laterally. Legs red-brown; female paler.

Genitalia. Male. (Fig. 360-364). (Specimen from St Hippolyte, Québec). Males distinguished by tergum X distal lobes, in dorsal aspect (Fig. 361), very slightly directed mesad; by distal tooth of aedeagus dorsal lobe, in lateral aspect (Fig. 363), with rounded base surmounted by much narrower rounded spine – not visible in dorsal aspect (Fig. 364); and by lateral lobe on posterior edge of segment IX set very low, connected to dorsum of segment by thin, dark line.

Genitalia. Female. (Fig. 365-366). (Specimen from St Hippolyte, Québec). Females distinguished by clasper receptacle directed dorsad in lateral aspect (Fig. 365), directed mesad in dorsal aspect (Fig. 366); by dorsal and ventral lobes, and cerci of segment XI very close; and by sclerotised strap of vulval scale long, not wide distally, sinuate.

Biology.— Larvae apparently inhabit rapids sections of smaller, cool, clear streams (Schuster & Etnier, 1978). Emergence in April. Few Canadian flight records range from June 5 to August 29.

Distribution.— Very scattered (Map 57), with isolated records from Tennessee, North Carolina, to Pennsylvania, Québec, and southern Manitoba.

Hydropsyche bifida Banks
Map 58; Fig. 367–373

Hydropsyche bifida Banks, 1905a:15; Betten, 1934:193; Milne, 1936:73; Denning, 1943:129; Ross, 1944:97; Schefter & Unzicker, 1984:331 (as synonym of *H. morosa*).
Symphitopsyche bifida; Schuster & Etnier, 1978:30.

See note at end of 'Introduction'.

Description.— Male fore-wing length 8.03 mm; pale golden brown, faintly irrorate. Antennae brownish yellow; basal nine flagellar annuli each with oblique, dark band. Vertex yellow-brown. Spurs straw-coloured; lateral member of middle and hind-leg pairs notably shorter than mesal companions; not so in female. Thorax yellow-brown. Legs yellow, to pale straw.

Genitalia. Male. (Fig. 367-371). (Specimen from Blindman R., Hwy 2, Ponoka, Alberta). Males distinguished by tergum X distal lobes set high on distal end of tergum, thin, almost pointed distally, curved slightly ventrad, in lateral aspect (Fig. 367); by basal article of clasper slender, especially at base, crooked in lateral aspect; by distal article of clasper with base as wide as basal article, then sharply tapered to distal half which is of even width, narrow, rounded distally; and by tooth of dorsal lobe of aedeagus curved slightly ventrad, small, clothed in minute dentitions.

Genitalia. Female. (Fig. 372-373). (Specimen from Blindman R., Hwy 2, Ponoka, Alberta). Females distinguished by clasper receptacle curved antero-dorsad in lateral aspect (Fig. 372), meso-posterad in dorsal aspect (Fig. 373); by mouth of receptacle with one groove on floor; and by cerci closer to dorsal lobe of segment XI than to ventral lobe.

Biology.— Larvae commonly collected in medium-sized creeks or small rivers with coarse gravel or small rock substrates, and high organic loading. Canadian flight season extends from May 22 to October 16, with bulk of records in June-July.

Distribution.— Widely distributed, from Great Slave Lk. and central British Columbia to Oklahoma, Tennessee, Vermont, and Québec (Map 58). In Canada, well recorded across Prairie Provinces, sparsely in British Columbia, north to near Great Slave Lk. In the east, it is known from western and southern Québec, and southern Ontario.
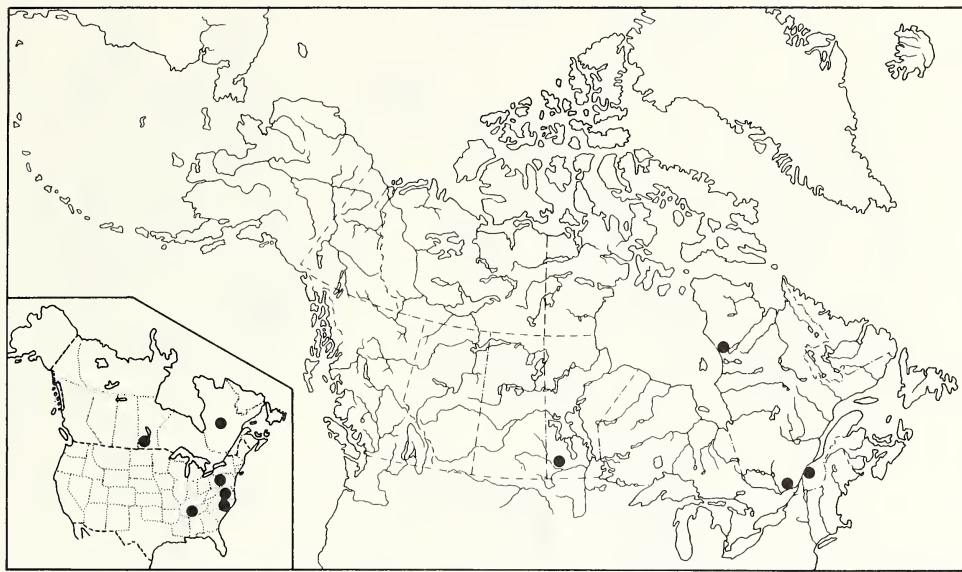
Map 57. Collection localities for *Hydropsyche alhedra* Ross in Canada, with known distribution in North America by state or province.
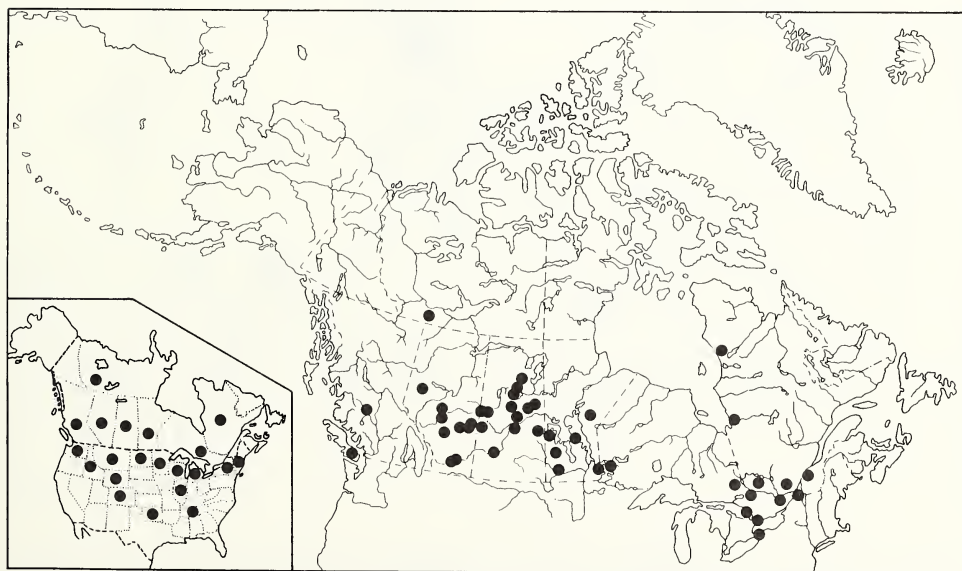
Map 58. Collection localities for *Hydropsyche bifida* Banks in Canada, with known distribution in North America by state or province.
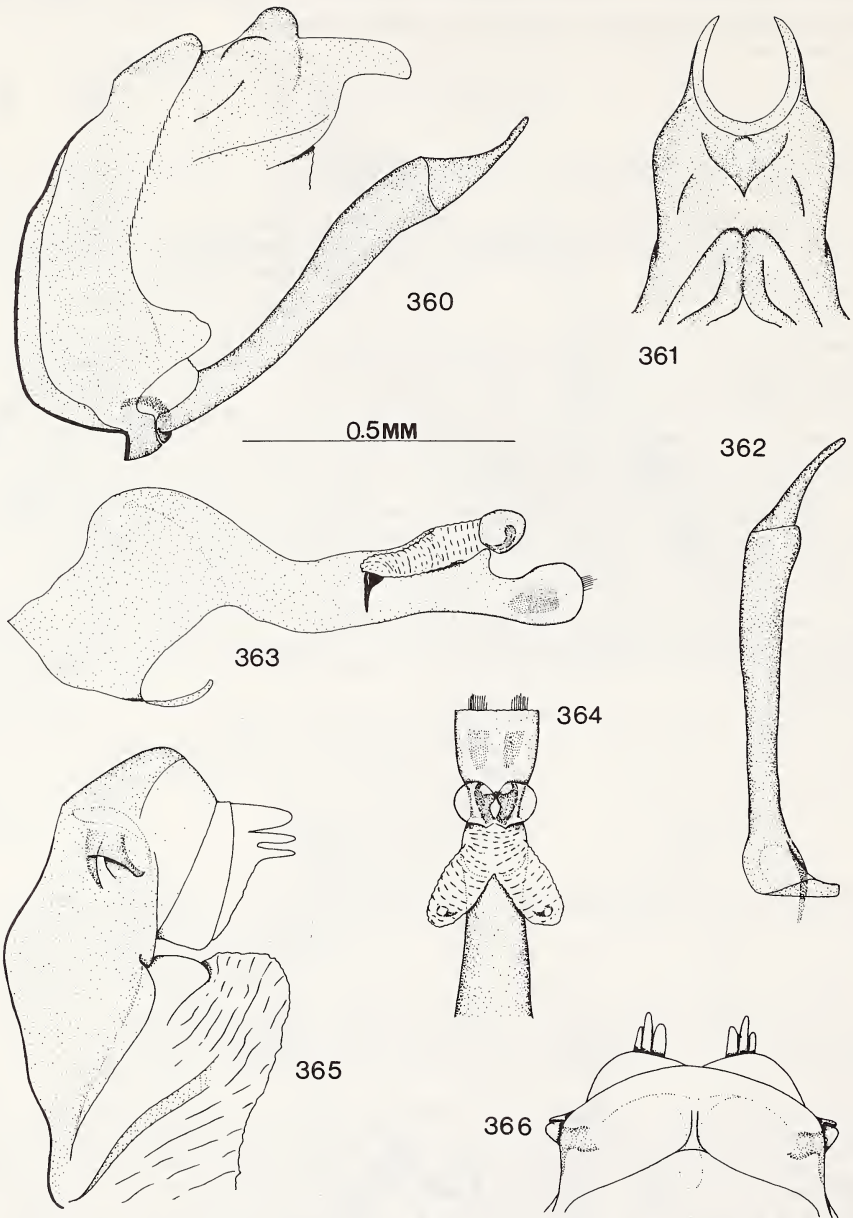
Fig. 360–366, *Hydropsyche alhedra* Ross: 360, genital capsule of male, lateral aspect; 361, genital capsule of male, dorsal aspect; 362, left clasper of male, posterior aspect; 363, aedeagus of male, lateral aspect; 364, aedeagus of male, dorsal aspect of tip; 365, genital segments of female, lateral aspect; 366, genital segments of female, dorsal aspect.
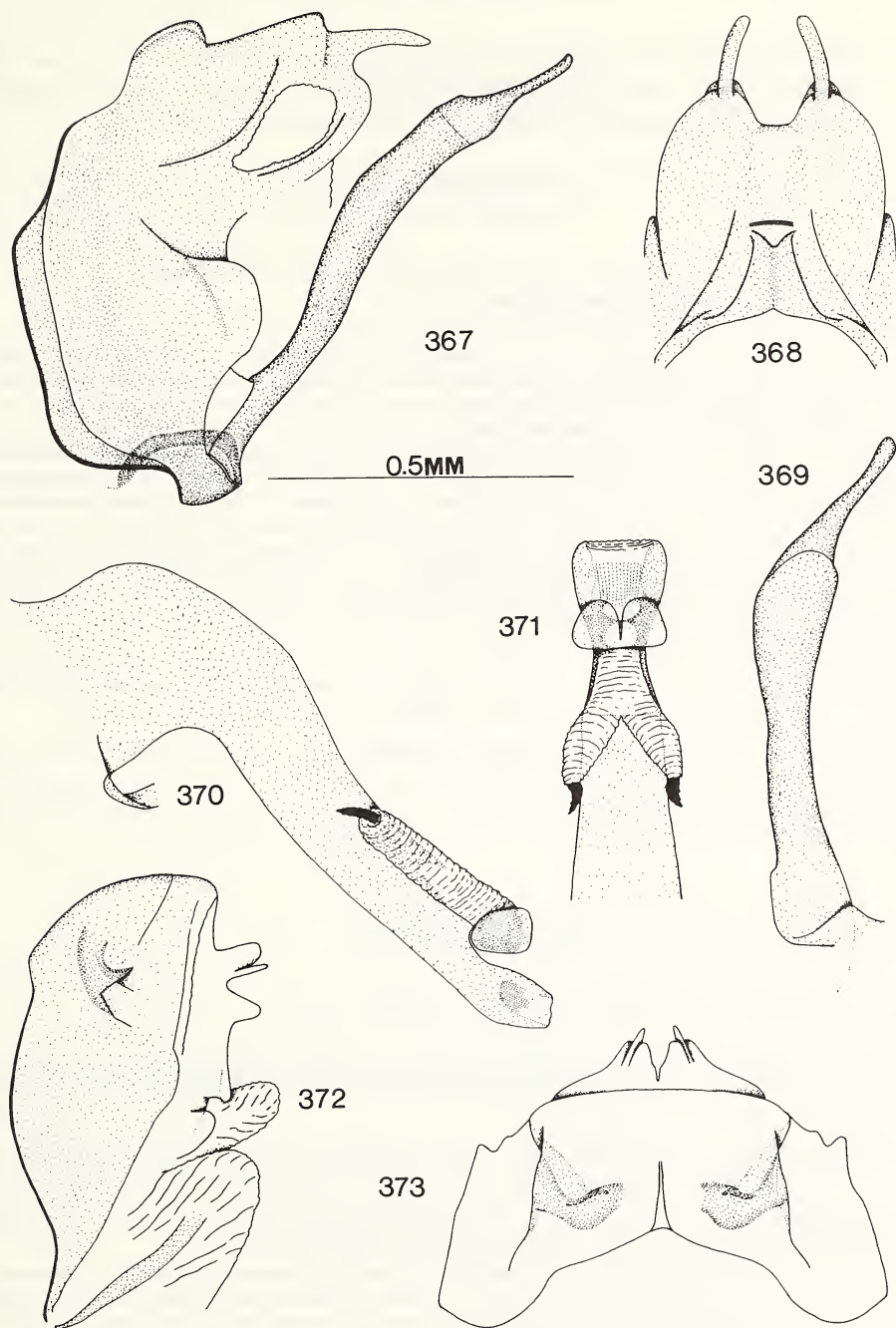
Fig. 367–373, *Hydropsyche bifida* Banks: 367, genital capsule of male, lateral aspect; 368, genital capsule of male, dorsal aspect; 369, left clasper of male, posterior aspect; 370, aedeagus of male, lateral aspect; 371, aedeagus of male, dorsal aspect of tip; 372, genital segments of female, lateral aspect; 373, genital segments of female, dorsal aspect.

SUBGROUP C

This group characterised by aedeagus not only with dorsal membranous lobes, but also with ventro-lateral lobes short, restricted to extreme distal portion of aedeagus; these lobes reduced in some species to simple, unsclerotised apertures laterally on aedeagus extremity.

Hydropsyche bronta Ross
Map 59; Fig. 374–380

Hydropsyche bronta Ross, 1938b:149; Denning, 1943:125; Ross, 1944:98; Schefter & Wiggins, 1986:52.
Symphitopsyche (Ceratopsyche) bronta; Ross & Unzicker, 1977:305.
Symphitopsyche bronta; Schuster & Etnier, 1978:37.

Description.— Male fore-wing length 7.29 mm; pale grey-brown, faintly irrorate; female pale orange-brown. Antennae brownish cream; apparently without oblique, dark bands in male; basal seven flagellar annuli of female each with faint, oblique, darker band. Spurs yellow-brown; lateral member of middle leg pairs notably shorter than mesal companions. Thorax and legs bright, pale yellow-brown overall.

Genitalia. Male. (Fig. 374–378). (Specimen from Carrot Ck, Hwy 16, Alberta). Males distinguished by distal article of clasper, in lateral aspect (Fig. 374), triangular, apex slightly drawn out; by tergum X distal lobes short in lateral aspect (Fig. 374), curved ventrad; by these lobes, in dorsal aspect (Fig. 375), short, linear, not convergent; and by dorsal lobe of aedeagus with large, stout, linear, distally acuminate distal tooth or spine directed antero-ventrad (Fig. 377).

Genitalia. Female. (Fig. 379–380). (Specimen from Ile Ste Hélène, St Lawrence R., Montréal, Québec). Females distinguished by clasper receptacle small, directed antero-dorsad in lateral aspect (Fig. 379), with outer margin of receptacle continued dorsad and ventrad by thin, dark lines; by inner opening of receptacle clearly evident in lateral aspect; and by receptacle, in dorsal aspect (Fig. 380), directed mesad.

Biology.— I have taken adults from a great variety of small creeks to medium-sized rivers, some cool, others warm, some clear, turbulent, others slow, weedy. Flight season ranges from May 25 to September 2, in Canada, with concentration of records in June and early July.

Distribution.— Widespread from Alberta and Wyoming, to South Carolina and Nova Scotia (Map 59). In Canada this species commonly recorded from Alberta lower foothills to eastern Québec, New Brunswick, and Nova Scotia, northward into southern reaches of Boreal Forest.

Hydropsyche cheilonis Ross
Map 60; Fig. 381–387

Hydropsyche cheilonis Ross, 1938b:149; Ross, 1944:98; Schefter & Wiggins, 1986:57.
Symphitopsyche cheilonis; Schuster & Etnier, 1978:33.

Description.— Male fore-wing length 7.80 mm; light purple-brown, slight irroration along A. Hind-wing tinted grey-brown. Antennae yellow; no banding on annuli. Vertex dark brown anteriorly, yellow posteriorly, warts dark brown. Spurs grey-brown; lateral member of fore- and hind-leg pairs shorter than mesal companions. Thorax mottled grey-brown and yellow-brown. Legs grey-brown to dull straw.

Genitalia. Male. (Fig. 381–385). (Specimen from Crossville, Cumberland Co., Tennessee, USA). Males distinguished by basal article of clasper, in lateral aspect (Fig. 381), sinuate, distal quarter wider than remainder; by distal article of clasper with trinagular base, with apex drawn out to finger-like process; by tergum X distal lobes, in dorsal aspect (Fig. 382), angled slightly mesad, linear; and by dorsal lobe of aedeagus with long, thin tooth or spine distally – tooth angled slightly ventrad at mid-point (Fig. 384), slightly expanded distally in dorsal aspect (Fig. 385).

Genitalia. Female. (Fig. 386–387). (Specimen from Beaver Ck, Knox Co., Tennessee, USA). Females distinguished by vulval scale with thin, curved primary sclerotised strap, and irregular, formless secondary sclerite laterally (Fig. 386); by clasper receptacle, in lateral aspect (Fig. 386), curved dorso-posterad, with two grooves on floor of outer opening; and by receptacle, in dorsal aspect (Fig. 387), curved meso-posterad.

Biology.— Larvae seem to prefer small to medium-sized, warm-water streams of slow current and large riffle areas. Emergence from early April to September.

Distribution.— Not yet known from Canada. Presently known from Wisconsin to Tennessee and Virginia (Map 60).

Hydropsyche morosa Hagen
Map 61; Fig. 388–394

Hydropsyche morosa Hagen, 1861:287; Milne, 1936:71, 73; Denning, 1943:127; Ross, 1944:98; Wiggins, 1977:106; Schefter & Unzicker, 1984:331; Schefter & Wiggins, 1986:62.
Hydropsyche chlorotica Hagen, 1861:290; Ross, 1938c:16 (as synonym of *H. morosa*).
Symphitopsyche morosa; Schuster & Etnier, 1978:41.

See note at end of 'Introduction'.

Description.— Male fore-wing length 9.63 mm; pale yellow-brown, faintly irrorate distally and along distal third of R1. Hind-wing hyaline. Antennae brown; with dark bands at each end of flagellar annuli. Vertex brown. Spurs brown. Thorax red-brown, to paler laterally. Legs light yellow-brown.
Genitalia. Male. (Fig. 388–392). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Males distinguished by distal article of clasper, in lateral aspect (Fig. 388), with wide base which supports long, finger-like distal process; by tergum X distal lobes, in dorsal aspect (Fig. 389), well separated, gently curved, thin, distally rounded; and by dorsal lobe of aedeagus with massive distal tooth, dorsal edge of which is spinate.
Genitalia. Female. (Fig. 393–394). (Specimen from Huberdeau, Québec). Females distinguished by clasper receptacle, in lateral aspect (Fig. 393), linear, directed dorso-anterad; by outer opening of receptacle with two lobes on floor of opening; and by receptacle, in dorsal aspect (Fig. 394), directed mesad.

Biology.— Apparently a species of medium-sized rivers with large riffle areas of small to medium rocks clothed in weed. Canadian flight season extends from May 16 to September 21.

Distribution.— Known from Cape Breton Island, Nova Scotia, west to Alberta, south to Tennessee (Map 61). In Canada the species is known from southern Ontario and Québec, with scattered records to north and west.

Hydropsyche slossonae Banks
Map 62; Fig. 395–401

Hydropsyche slossonae Banks 1905a:14; Betten, 1934:185 (as synonym of *H. alternans*); Milne, 1936:69, 72, 73; Denning, 1943:131; Ross, 1944:99; Schefter & Wiggins, 1986:70.
Symphitopsyche slossonae; Schuster & Etnier, 1978:47.

Description.— Male fore-wing length 9.36 mm; grey-brown, more or less irrorate. Antennae yellow-brown; basal seven flagellar annuli each with oblique, dark band; five in female. Vertex brown anteriorly, to pale yellow-brown posteriorly; dark brown with white warts in female. Spurs yellow; lateral member of middle leg pairs notably shorter than mesal companions. Thorax brown, to brownish yellow laterally; dark brown to grey-brown laterally in female. Legs pale brown, except hind-legs pale straw; uniform yellow-brown in female.
Genitalia. Male. (Fig. 395–399). (Specimen from Rapids Ck, Trans-Canada Hwy, Gap, Alberta). Males distinguished by massive distal lobes of tergum X, in lateral aspect (Fig. 395), tapered rather abruptly in distal half; by these lobes, in dorsal aspect (Fig. 396), lyre-like; and by dorsal lobe of aedeagus small, abruptly tapered anterad, with minute distal tooth (Fig. 398).
Genitalia. Female. (Fig. 400–401). (Specimen from creek, Hwy 932, 6 miles S of Whitecourt, Alberta). Females distinguished by clasper receptacle, in lateral aspect (Fig. 400), oriented vertically, curved dorso-posterad distally, with two grooves on floor of outer opening; and by dorsal and ventral lobes of segment XI, and cerci, all visible in dorsal aspect (Fig. 401).

Biology.— A species of cold-water streams; little more known of larval habitat preferences. Canadian flight records range from June 6 to September 5, with peak of sorts in late June and July.

Distribution.— Widespread from eastern seaboard of North America to northwestern North America (Great Slave Lake and central British Columbia) (Map 62). Recorded in Canada from Newfoundland to Great Slave Lk, central British Columbia, south to United States border.

Hydropsyche tana Ross
Map 63; Fig. 402–408

Hydropsyche tana Ross, 1938b:151; Ross, 1944:294; Schefter & Wiggins, 1986:77.

Description.— Male fore-wing length 8.42 mm; grey-brown, fairly uniformly irrorate. Antennae brownish straw; basal seven flagellar annuli each with oblique, dark band. Vertex dark brown, posterior warts paler. Spurs yellow; lateral member of middle and hind-leg pairs much shorter than mesal companions. Thorax dark brown, to grey-brown laterally. Legs straw-coloured.

Genitalia. Male. (Fig. 402–406). (Specimen from creek, Hwy 37, 92 km N of Kitwanga, British Columbia). Males distinguished by tergum X distal lobes, in lateral aspect (Fig. 402), massive, with narrower tip directed postero-ventrad; by these lobes, in dorsal aspect (Fig. 403), curved postero-mesad; by distal article of clasper tapered slightly distad, with dorsal edge of tip scalloped (Fig. 402); and by dorsal lobe of aedeagus (Fig. 405) with tooth (wide-based, with distal spine) directed postero-laterad (Fig. 406).

Genitalia. Female. (Fig. 407–408). (Specimen from Teton R., Tetonia, Teton Co., Idaho, USA). Females distinguished by clasper receptacle minute, set very high on lateral wall of segment X (Fig. 407); and by outer margin of receptacle bowed distinctly ventrad.

Biology.— Nothing known, except known flight dates range from July 1 to 16.

Distribution.— Presently known only from western Montana, Idaho, British Columbia, and Vancouver Island (Map 63). In Canada, recorded from just north of Skeena R., southern Vancouver Island, and interior British Columbia.
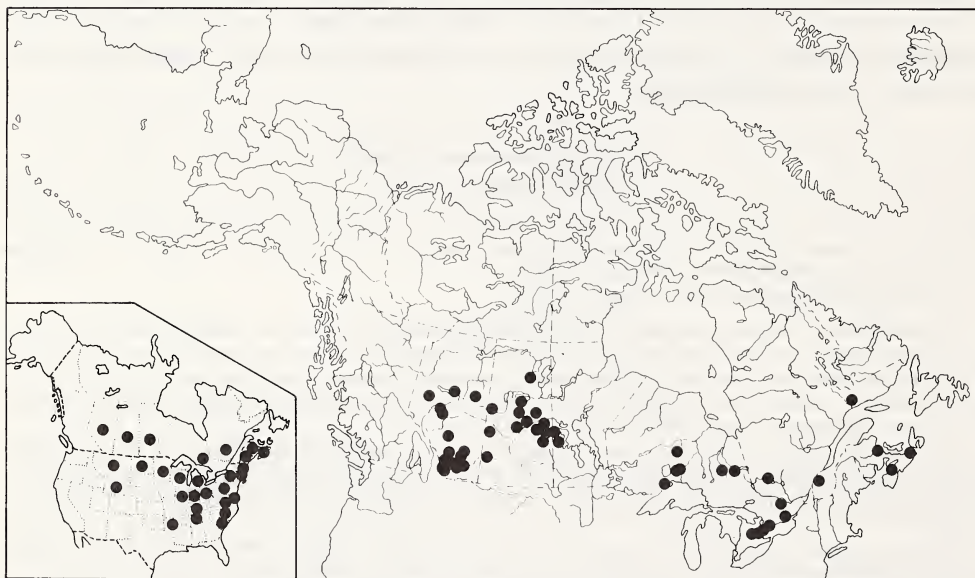
Map 59. Collection localities for *Hydropsyche bronta* Ross in Canada, with known distribution in North America by state or province.

Map 60. Known distribution of *Hydropsyche cheilonis* Ross in North America, by state.
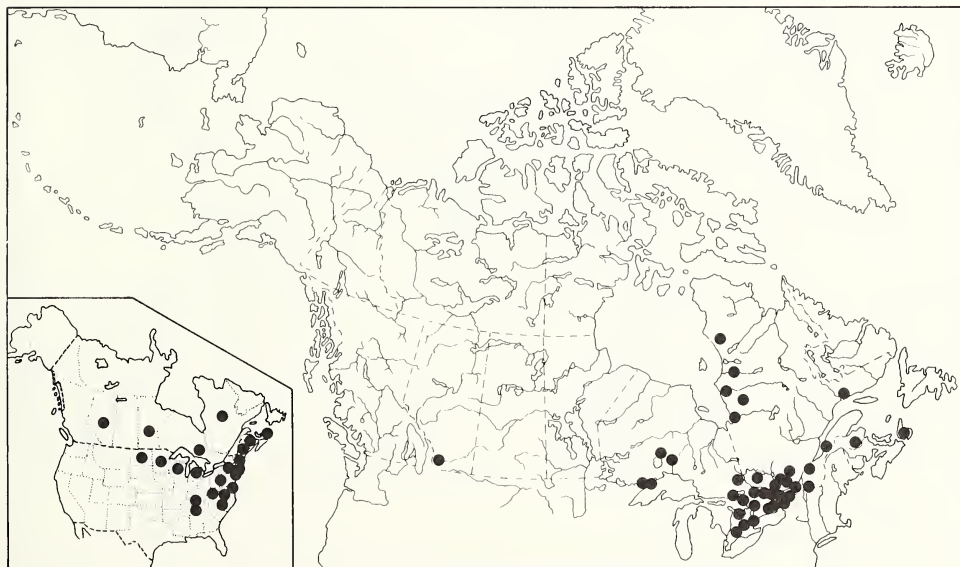
Map 61. Collection localities for *Hydropsyche morosa* Hagen in Canada, with known distribution in North America by state or province.
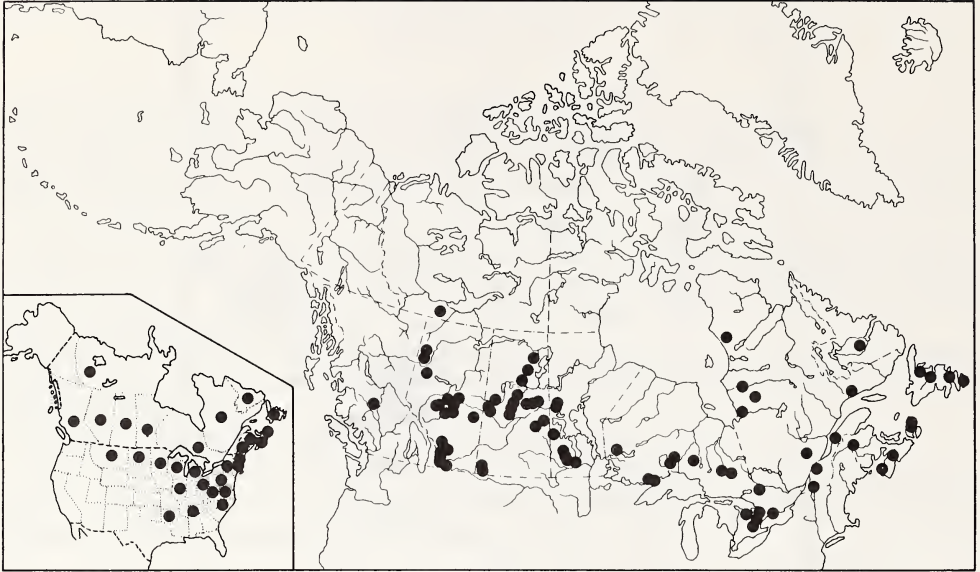
Map 62. Collection localities for *Hydropsyche slossonae* Banks in Canada, with known distribution in North America by state or province.
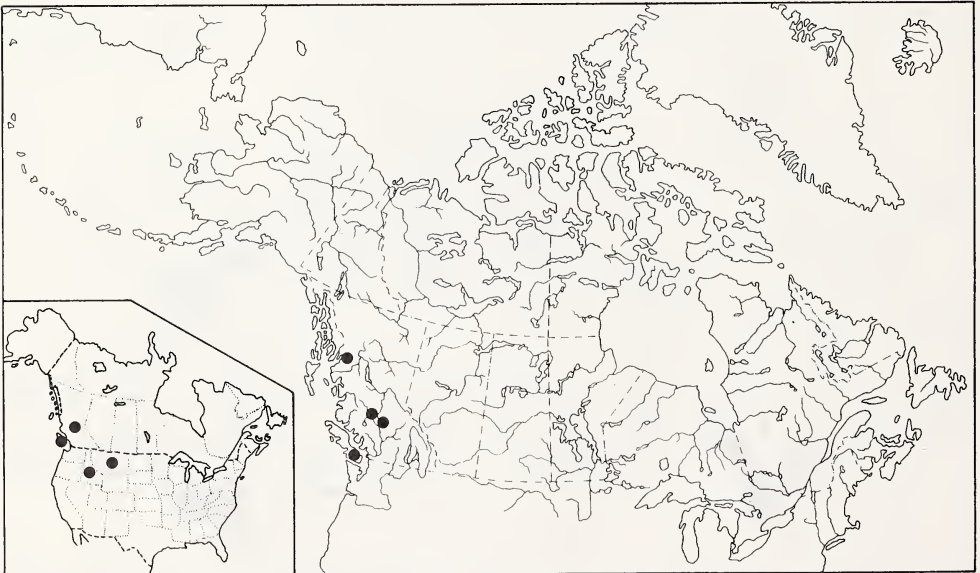
Map 63. Collection localities for *Hydropsyche tana* Ross in Canada, with known distribution in North America by state or province.
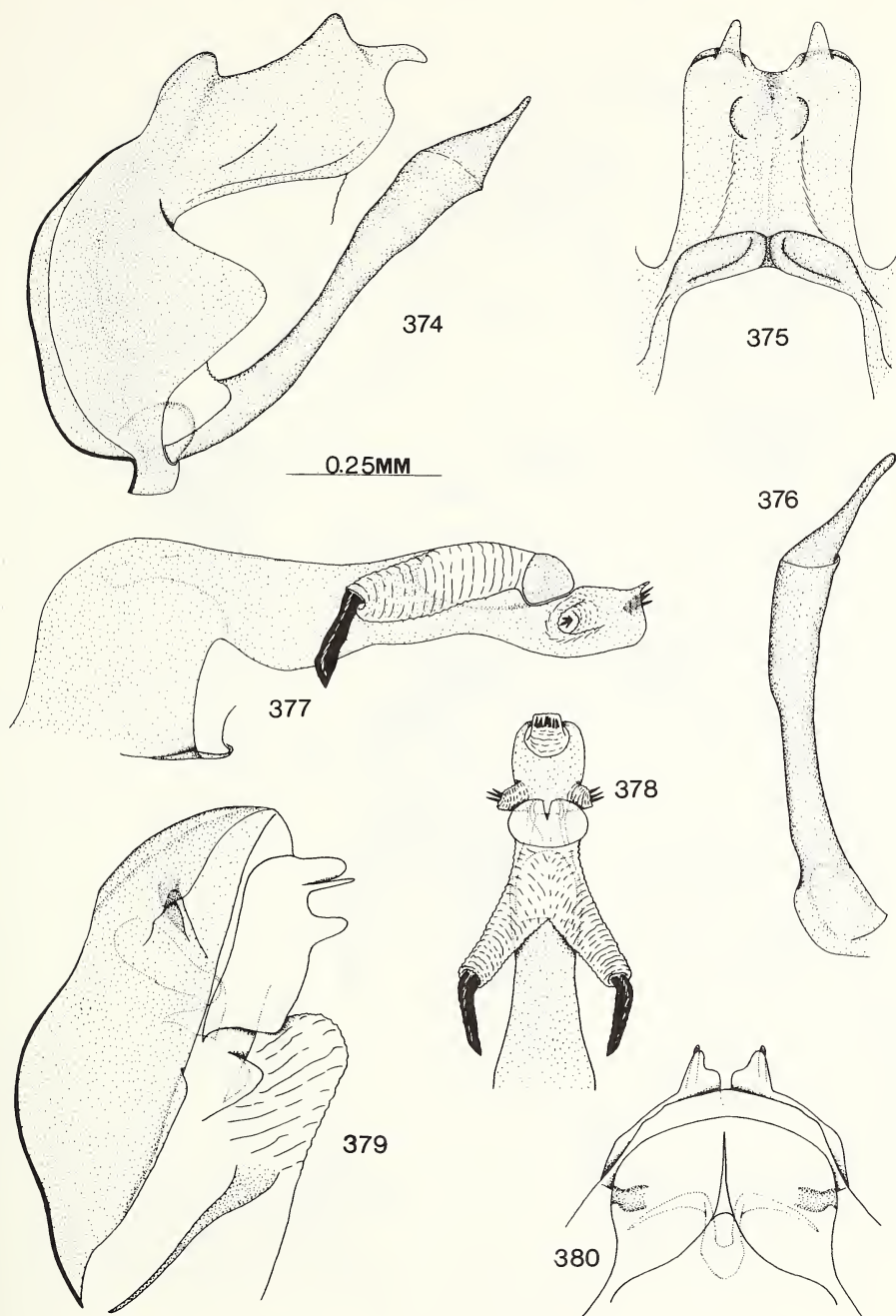
Fig. 374–380, *Hydropsyche bronta* Ross: 374, genital capsule of male, lateral aspect; 375, genital capsule of male, dorsal aspect; 376, left clasper of male, posterior aspect; 377, aedeagus of male, lateral aspect; 378, aedeagus of male, dorsal aspect of tip; 379, genital segments of female, lateral aspect; 380, genital segments of female, dorsal aspect.
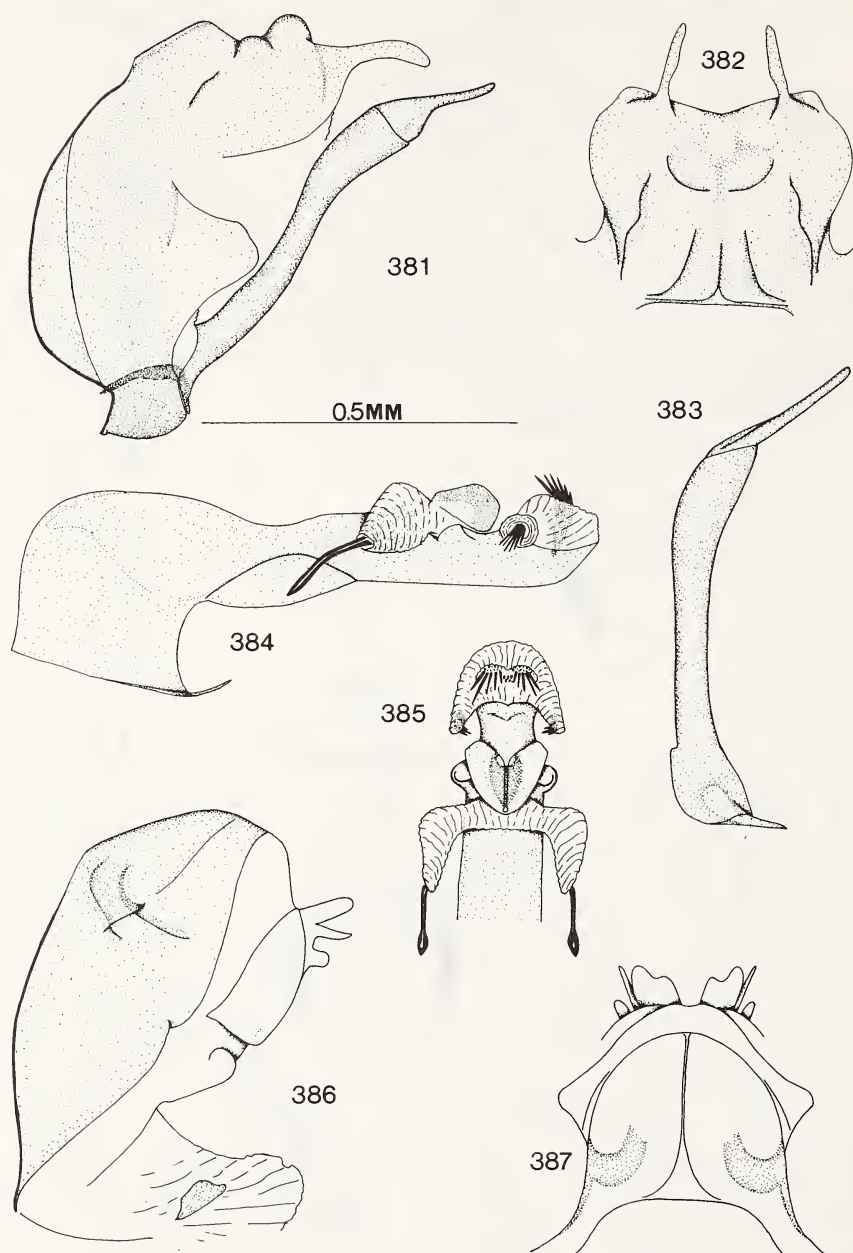
Fig. 381–387, *Hydropsyche cheilonis* Ross: 381, genital capsule of male, lateral aspect; 382, genital capsule of male, dorsal aspect; 383, left clasper of male, posterior aspect; 384, aedeagus of male, lateral aspect; 385, aedeagus of male, dorsal aspect of tip; 386, genital segments of female, lateral aspect; 387, genital segments of female, dorsal aspect.

0.5MM
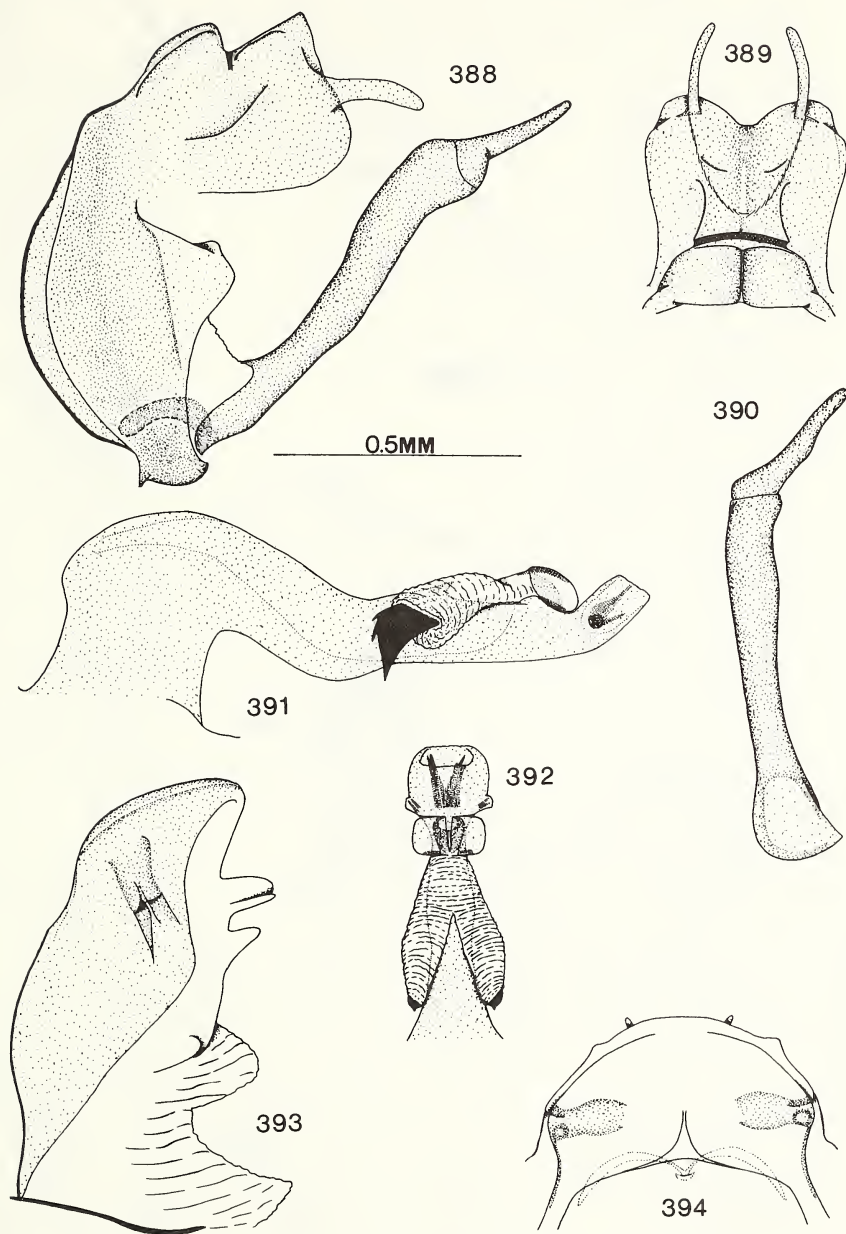
Fig. 388–394, *Hydropsyche morosa* Hagen: 388, genital capsule of male, lateral aspect; 389, genital capsule of male, dorsal aspect; 390, left clasper of male, posterior aspect; 391, aedeagus of male, lateral aspect; 392, aedeagus of male, dorsal aspect of tip; 393, genital segments of female, lateral aspect; 394, genital segments of female, dorsal aspect.
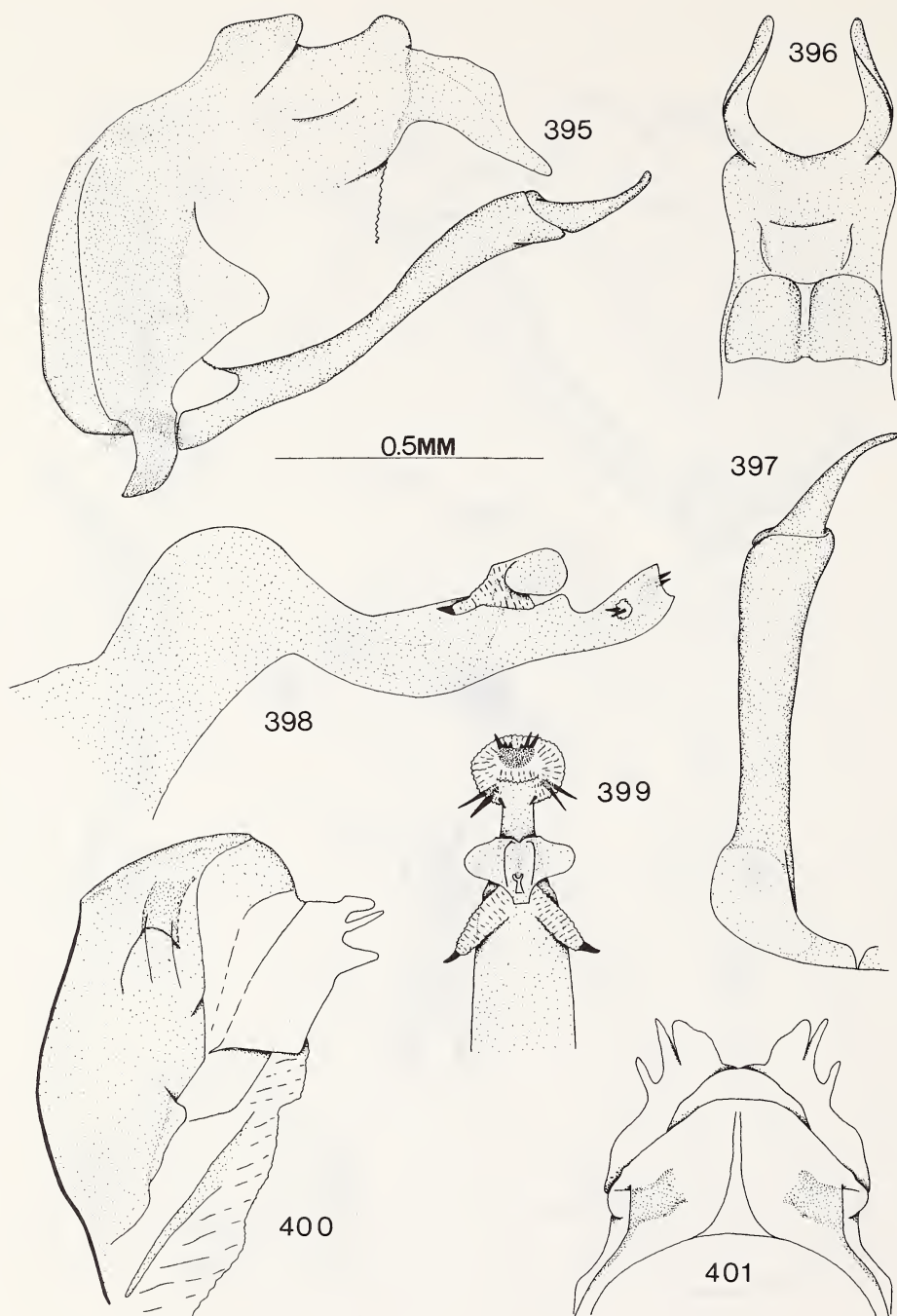
Fig. 395–401, *Hydropsyche slossonae* Banks: 395, genital capsule of male, lateral aspect; 396, genital capsule of male, dorsal aspect; 397, left clasper of male, posterior aspect; 398, aedeagus of male, lateral aspect; 399, aedeagus of male, dorsal aspect of tip; 400, genital segments of female, lateral aspect; 401, genital segments of female, dorsal aspect.

0.25MM

Fig. 402–408, *Hydropsyche tana* Ross: 402, genital capsule of male, lateral aspect; 403, genital capsule of male, dorsal aspect; 404, left clasper of male, posterior aspect; 405, aedeagus of male, lateral aspect; 406, aedeagus of male, dorsal aspect of tip; 407, genital segments of female, lateral aspect; 408, genital segments of female, dorsal aspect.

SUBGROUP D

This group characterised by aedeagus with dorsal membranous lobes only, distal teeth, or spines, of which are curved antero-dorsad.

Hydropsyche aenigma Schefter, Wiggins, & Unzicker

Hydropsyche aenigma Schefter, Wiggins, & Unzicker, 1986:78; Schefter & Wiggins, 1986:44.

This species, described from New York State in 1986, is very close to *H. alternans* (Walker) and *H. centra* Ross. Time constraints precluded inclusion of illustrations here, but comparative illustrations of all three species are given by the authors.

Hydropsyche alternans (Walker)
Map 64; Fig. 409–415

Philopotamus alternans Walker, 1852:104.
Hydropsyche alternans; Vorhies, 1909:707 (sp. indet.); Betten, 1934:185 (prob. *H. bifida*); Nimmo, 1981:261 (*H. recurvata* as synonym); Schefter & Wiggins, 1986:48.
Hydropsyche slossonae var. *recurvata* Banks, 1914:253.
Hydropsyche recurvata; Betten, 1934:190; Milne, 1936:73 (as synonym of *H. slossonae*); Denning, 1943:126; Ross, 1944:99; Schmid, 1980:Fig. 131-140; Nimmo, 1981:261 (as synonym of *H. alternans*).
Symphitopsyche recurvata; Schuster & Etnier, 1978:34.
Hydropsyche codona Betten, 1934:187; Milne, 1936:73 (as synonym of *H. slossonae*); Ross, 1938c:18 (as synonym of *H. recurvata*).

Description.— Male fore-wing length 9.44 mm; grey-brown, clearly irrorate. Hind-wing faintly tinted brown. Antennae pale brown; basal eight flagellar annuli each with oblique, dark band. Vertex dark brown anteriorly, yellow-brown posteriorly. Spurs pale yellow-brown, to straw; lateral member of middle leg pairs notably shorter than mesal companions. Thorax dark brown, to paler laterally.

Genitalia. Male. (Fig. 409–413). (Specimen from Wandering R., Hwy 63, Wandering River, Alberta). Males distinguished by distal article of clasper, in posterior aspect (Fig. 411), acute-triangular; by small, membranous, dorsally directed lobe located dorsally on aedeagus, between two dorsal lobes (Fig. 412); and by tergum X distal lobes narrow, well separated, acuminate, in dorsal aspect (Fig. 410).

Genitalia. Female. (Fig. 414–415). (Specimen from Wandering R., Hwy 63, Wandering River, Alberta). Females distinguished by clasper receptacle, in lateral aspect (Fig. 414), directed antero-dorsad, like inverted vase due to swelling; by outer opening of receptacle with two grooves on floor; and by receptacle, in dorsal aspect (Fig. 415), directed antero-mesad.

Biology.— Commonly collected from fast, cold waters, but known from warmer waters also. Known from small creeks, to largest rivers, suggesting wide tolerance of habitat types. Ross (1944) also records larvae from wave-washed shores of large lakes. Flight season ranges from May 8 to October 16 in Canada, with peak in June/July.

Distribution.— Very widespread, known from Alaska to Newfoundland, south to southern British Columbia, St Lawrence R. valley in Canada, and to most states in United States, about the Great Lakes (Map 64).

Hydropsyche centra Ross
Map 65; Fig. 416–422

Hydropsyche centra Ross, 1938b:150; Ross, 1944:294; Anderson, 1976:66; Schefter & Wiggins, 1986:55.

Description.— Male fore-wing length 9.36 mm; uniform pale yellowish brown, faintly irrorate posterad of Cu1+2; irroration not evident in females seen. Hind-wing hyaline; pale reddish brown in female. Antennae pale yellow-brown; basal seven flagellar annuli each with oblique, dark band. Vertex almost black, warts paler; dark red-brown to chocolate in female. Spurs pale yellow-brown; lateral member of middle leg pairs shorter than mesal companions. Thorax very deep red-brown, to paler laterally. Legs pale yellow to straw.

Genitalia. Male. (Fig. 416–420). (Specimen from Leaburg Dam, Mackenzie R., Lake Co., Oregon, USA). Males distinguished by lobe on postero-ventral edge of segment IX long, narrow at base, rounded distally (Fig. 416); by tergum X distal lobes, in dorsal aspect (Fig. 417), curved mesad with oval gap between lobes; and by teeth or spines of dorsal lobes of aedeagus, in lateral aspect (Fig. 419), large, with short, straight base, with distal portion long, curved antero-dorsad from base, acuminate.

Genitalia. Female. (Fig. 421–422). (Specimen from Lakelse, 18 miles of S Terrace, British Columbia). Females distinguished by small clasper receptacle, in lateral aspect (Fig. 421), directed dorsad, distally rounded, without inner opening visible; and by receptacle, in dorsal aspect (Fig. 422), directed meso-anterad.

Biology.— Little known. Flight season records for Oregon (Anderson, 1976) range from late April to late September, with peak in May/June. The few Canadian records fall within this range.

Distribution.— Presently known only from Oregon, Washington, British Columbia, Vancouver Island (Map 65). In British Columbia the species has been recorded as far north as Skeena R. basin.

Hydropsyche cockerelli Banks
Map 66; Fig. 423–429

Hydropsyche cockerelli Banks, 1905a:14; Betten, 1934:193; Milne, 1936:70, 71, 73; Ross, 1944:294; Schefter, Wiggins, & Unzicker, 1986:73; Schefter & Wiggins, 1986:58.

See note at end of 'Introduction'.

Description.— Male fore-wing length 8.74 mm; pale greyish brown, faintly irrorate; female more orange-brown. Hind-wing faintly tinted brown. Antennae pale yellow-brown; basal eight flagellar annuli each with oblique, dark band. Vertex dark brown. Lateral member of middle and hind-leg spur pairs rather shorter than mesal companions. Thorax dark reddish brown, to brown laterally. Legs yellowish cream.

Genitalia. Male. (Fig. 423–427). (Specimen from Waterton R., Hwy 5, Alberta). Males distinguished by tergum X distal lobes, in lateral aspect (Fig. 423), directed postero-dorsad, with disto-dorsal angle produced as rounded, triangular point; by these lobes, in dorsal aspect (Fig. 424), curved postero-laterad; and by distal article of clasper, in lateral aspect (Fig. 423), skewed acute-triangular, with tip hooked slightly dorsad.

Genitalia. Female. (Fig. 428–429). (Specimen from Waterton R., Hwy 5, Alberta). Females distinguished by very small clasper receptacle, in lateral aspect (Fig. 428), directed dorso-anterad, with outer margin located at mid-point of receptacle; by receptacle, in dorsal aspect (Fig. 429), directed sharply anterad; and by sclerotised strap of vulval scale large, widest at two-thirds distance from proximal end.

Biology.— Larvae seem to exhibit wide latitude in choice of habitat. Recorded from small, sluggish prairie streams, from very large cordilleran rivers, and all sizes of foothills streams. Flight season ranges from May 20 to September 5 in Canada, with no very obvious peak. Anderson (1976) records the peak of emergence in Oregon as August/September.

Distribution.— Recorded from New Mexico, California, to southern Yukon (Map 66). In Canada, widely recorded from plains and near-foothills areas of Alberta, with scattered records from British Columbia, and Whitehorse, Yukon.

Hydropsyche jewetti Denning
Map 67; Fig. 430–434

Hydropsyche jewetti Denning, 1965:78; Schefter, Wiggins, & Unzicker, 1986:73 (as synonym of *H. cockerelli*).

See note at end of 'Introduction'.

Description.— Male fore-wing length 10.14 mm; golden brown, faintly irrorate. Hind-wing very pale gold. Antennae pale brownish yellow; basal nine flagellar annuli each with oblique, dark band. Vertex deep chocolate, slightly paler posteriorly. Spurs pale yellow-brown; lateral member of middle leg pairs markedly shorter than mesal companions. Thorax dark chocolate-brown, to lighter laterally. Legs pale straw.

Genitalia. Male. (Fig. 430–434). (Specimen from 1-mile Ck, Hwy 5, N of Princeton, British Columbia). Males distinguished by tergum X distal lobes, in lateral aspect (Fig. 430), directed postero-dorsad, slightly cleft distally to two rounded lobes; by distal article of clasper, in lateral aspect, acute-triangular; by tergum X distal lobes, in dorsal aspect (Fig. 431), short, acuminate, with tips turned slightly mesad; and by distal teeth of aedeagus dorsal lobes small, curved

only slightly at base (Fig. 433).

Genitalia. Female. Unknown.

Biology.— Almost nothing known. 1-mile Creek is a small, rocky stream flanked by Poplar and farmland. Date of collection was July 13. Newell & Potter (1973) give June/July as Montana flight season.

Distribution.— Presently known only from western Montana and south-central British Columbia (Map 67).
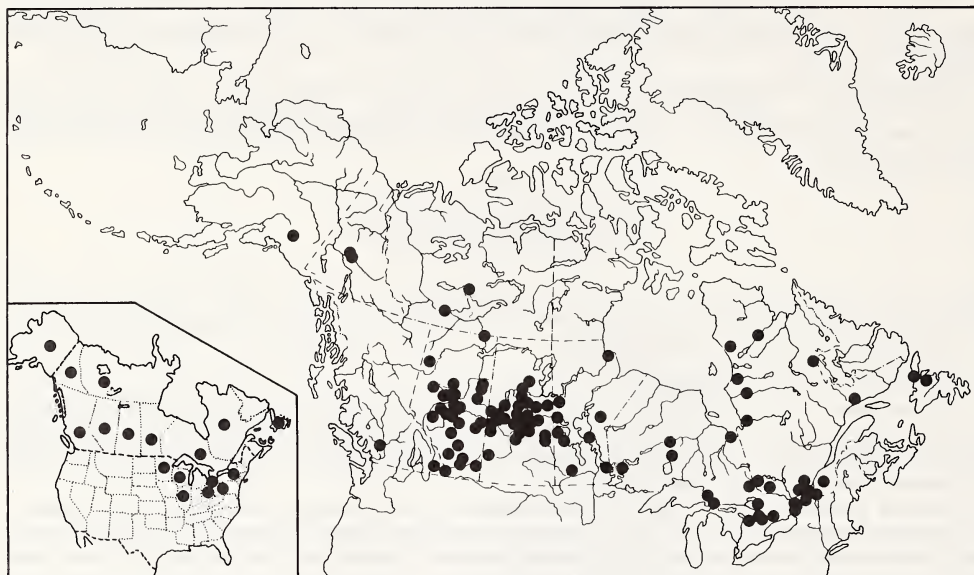
Map 64. Collection localities for *Hydropsyche alternans* (Walker) in Canada and Alaska, with known distribution in North America by state or province.
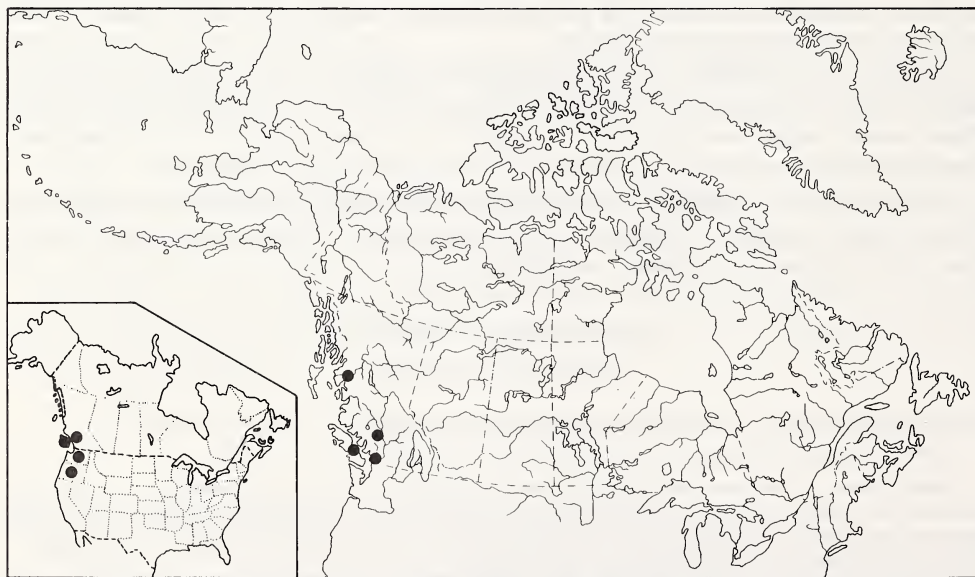
Map 65. Collection localities for *Hydropsyche centra* in Canada, with known distribution in North America by state or province.
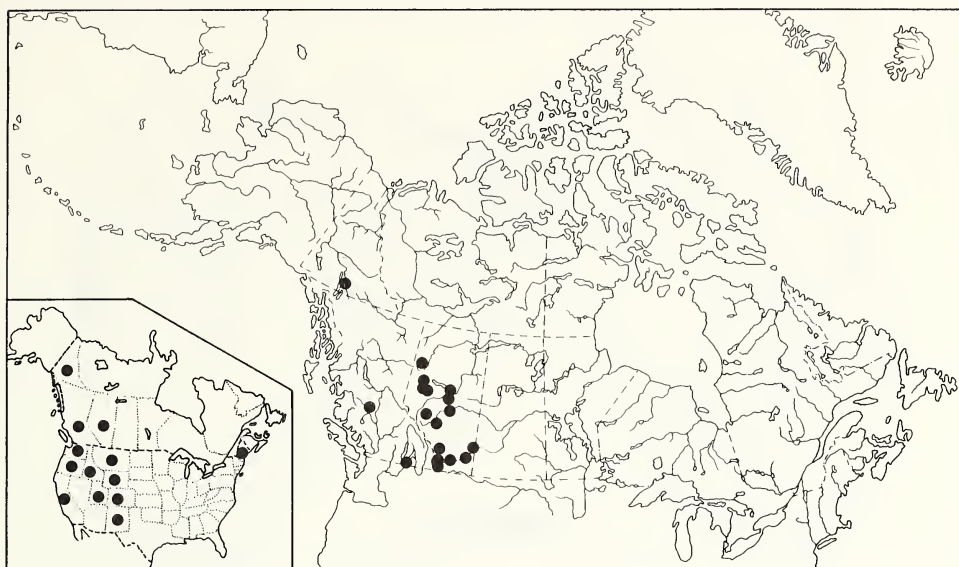
Map 66. Collection localities for *Hydropsyche cockerelli* Banks in Canada, with known distribution in North America by state or province.

Map 67. Collection localities for *Hydropsyche jewetti* Denning in Canada, with known distribution in North America by state or province.

Fig. 409–415, *Hydropsyche alternans* (Walker): 409, genital capsule of male, lateral aspect; 410, genital capsule of male, dorsal aspect; 411, left clasper of male, posterior aspect; 412, aedeagus of male, lateral aspect; 413, aedeagus of male, dorsal aspect of tip; 414, genital segments of female, lateral aspect; 415, genital segments of female, dorsal aspect.
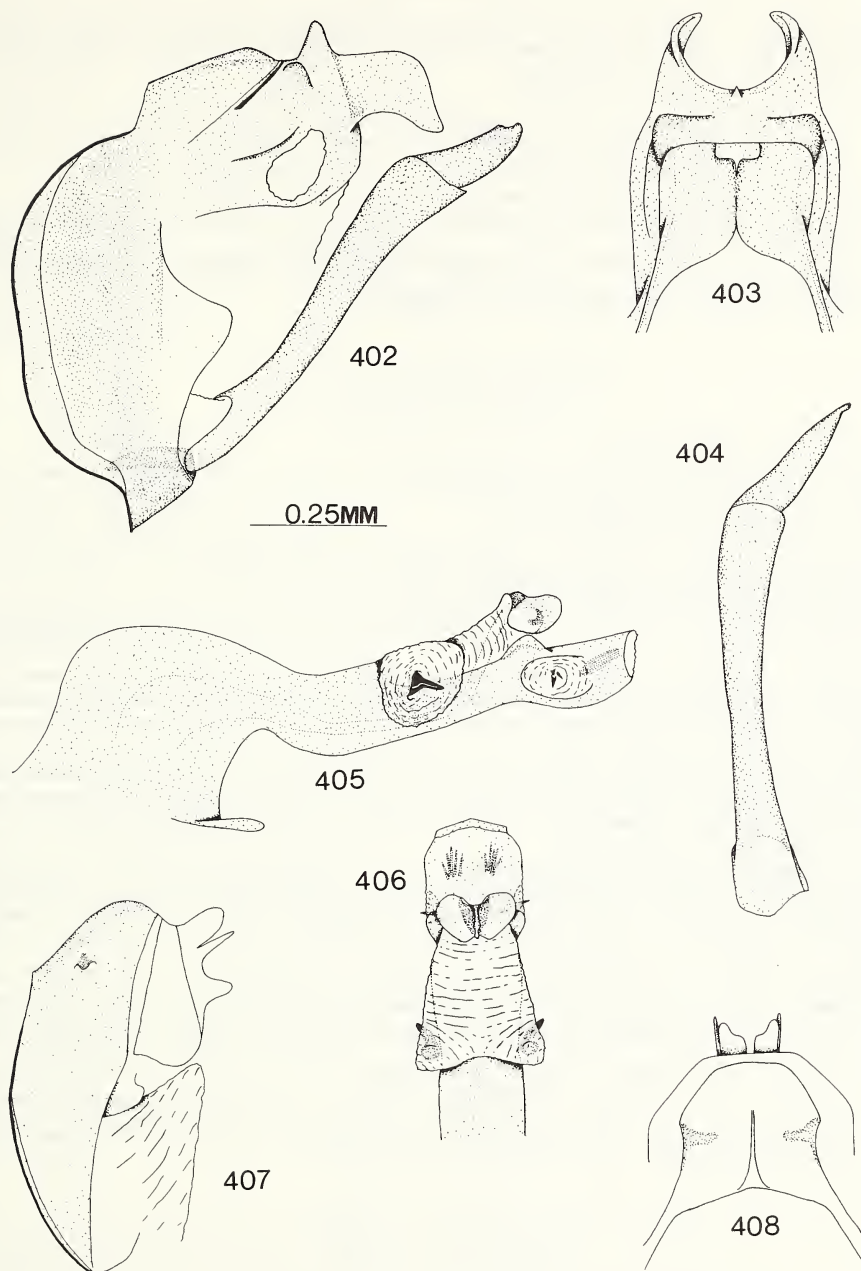
Fig. 416–422, *Hydropsyche centra* Ross: 416, genital capsule of male, lateral aspect; 417, genital capsule of male, dorsal aspect; 418, left clasper of male, posterior aspect; 419, aedeagus of male, lateral aspect; 420, aedeagus of male, dorsal aspect of tip; 421, genital segments of female, lateral aspect; 422, genital segments of female, dorsal aspect.

0.5MM

Fig. 423–429, *Hydropsyche cockerelli* Banks: 423, genital capsule of male, lateral aspect; 424, genital capsule of male, dorsal aspect; 425, left clasper of male, posterior aspect; 426, aedeagus of male, lateral aspect; 427, aedeagus of male, dorsal aspect of tip; 428, genital segments of female, lateral aspect; 429, genital segments of female, dorsal aspect.

Fig. 430–434, *Hydropsyche jewetti* Denning: 430, genital capsule of male, lateral aspect; 431, genital capsule of male, dorsal aspect; 432, left clasper of male, posterior aspect; 433, aedeagus of male, lateral aspect; 434, aedeagus of male, dorsal aspect of tip.

SUBGROUP E

This subgroup characterised by aedeagus dorsal lobes with one large tooth (distally & laterally), and cluster of small spines (laterally & distally).

Hydropsyche riola Denning
Map 68; Fig. 435–441

Hydropsyche riola Denning, 1942:49; Denning, 1943:133; Ross, 1944:294; Schefter, Wiggins, & Unzicker, 1986:69 (as synonym of *H. alhedra*).
Symphitopsyche riola; Schuster & Etnier, 1978:44.

See note at end of 'Introduction'.

Description.— Male fore-wing length 9.52 mm; bright grey-brown, with alternate areas of colour and hyaline membrane; female more generally irrorate. Antennae brown; basal eight flagellar annuli each with oblique, dark band. Vertex deep brown anteriorly, to deep orange-brown posteriorly. Spurs yellow-brown; lateral member of middle and hind-leg pairs notably shorter than mesal companions. Thorax deep brown. Legs brownish yellow to straw.

Genitalia. Male. (Fig. 435–439). (Specimen from creek, Hwy 932, 6 miles S of Whitecourt, Alberta). Males distinguished by tergum X distal lobes, in dorsal aspect (Fig. 436), close together, long, evenly tapered, curved slightly mesad, with long elliptical gap between; by basal article of clasper, in posterior aspect (Fig. 437), with very narrow basal half; and by aedeagus dorsal lobe, in lateral aspect (Fig. 438), with long, slender, acuminate tooth distally, and cluster of spines mid-way to tooth, on posterior face of lobe.

Genitalia. Female. (Fig. 440–441). (Specimen from creek, Hwy 932, 6 miles S of Whitecourt, Alberta). Females distinguished by clasper receptacle, in dorsal aspect (Fig. 441), directed mesad; by receptacle, in lateral aspect (Fig. 440), traversed by thin, dark line from dorsum of segment X; and by sclerotised strap of vulval scale long, sinuate, widened distally.

Biology.— My records indicate that larvae are not especially restricted in stream types occupied. Adult collecting sites include sluggish, silty prairie streams; turbulent, boulder-bottomed small rivers; smooth-flowing, earth-banked boreal creeks; and weed-filled streamlets. Flight season records range from May 25 to August 8, in Canada.

Distribution.— Recorded in narrow zone across North America from Massachusetts to Alaska (Map 68). Other than in Saskatchewan and Alberta, the known distribution is disjointed.

Hydropsyche sparna Ross
Map 69; Fig. 442–448

Hydropsyche sparna Ross, 1938b:150; Denning, 1943:134; Ross, 1944:97; Schefter & Wiggins, 1986:74.
Symphitopsyche sparna; Schuster & Etnier, 1978:52.

Description.— Male fore-wing length 8.27 mm; pale golden brown, no patter evident. Hind-wing faintly tinted golden brown. Antennae yellow; no dark banding on flagellar annuli. Vertex brownish yellow; orange-brown in female. Spurs yellow; lateral member of middle leg pairs markedly shorter than mesal companions. Thorax brownish yellow; orange-brown in female. Legs yellow to straw.

Genitalia. Male. (Fig. 442–446). (Specimen from Flanders, Morris Co., New Jersey, USA). Males distinguished by distal article of clasper, in lateral aspect (Fig. 442), abruptly narrowed, from wide base, to long, thin, slightly curved process; by tergum X distal lobes, in dorsal aspect (Fig. 443), directed posterad, slightly twisted, with wide, u-shaped gap between; and by aedeagus dorsal lobe, in lateral aspect (Fig. 445), with distal cluster of spines, and tooth (wide-based, abruptly narrowed to distal spine) located at mid-point on posterior face.

Genitalia. Female. (Fig. 447–448). (Specimen from Flanders, Morris Co., New Jersey, USA). Females distinguished by clasper receptacle, in lateral aspect (Fig. 447), with thin, dark line from dorsum of segment X terminated at dorsal extremity of receptacle; by receptacle, in dorsal aspect (Fig. 448), directed postero-mesad; and by vulval scale sclerotised strap thin, angled.

Biology.— Larvae exhibit wide ecological tolerance, from sluggish, small, organically rich streams, to fast, clear, cold trout-stream waters (Schuster & Etnier, 1978). Canadian flight season ranges from May 17 to September 26, with bulk of records from August.

Distribution.— Predominantly an eastern species, recorded from Georgia to Newfoundland, west across the Appalachians, with extension from Michigan to Manitoba (Map 69). In Canada, known from Duck Mountain Provincial Park, on western boundary of Manitoba, to Labrador and Newfoundland. From the above it may be surmised that the species is confined to woodland waters.
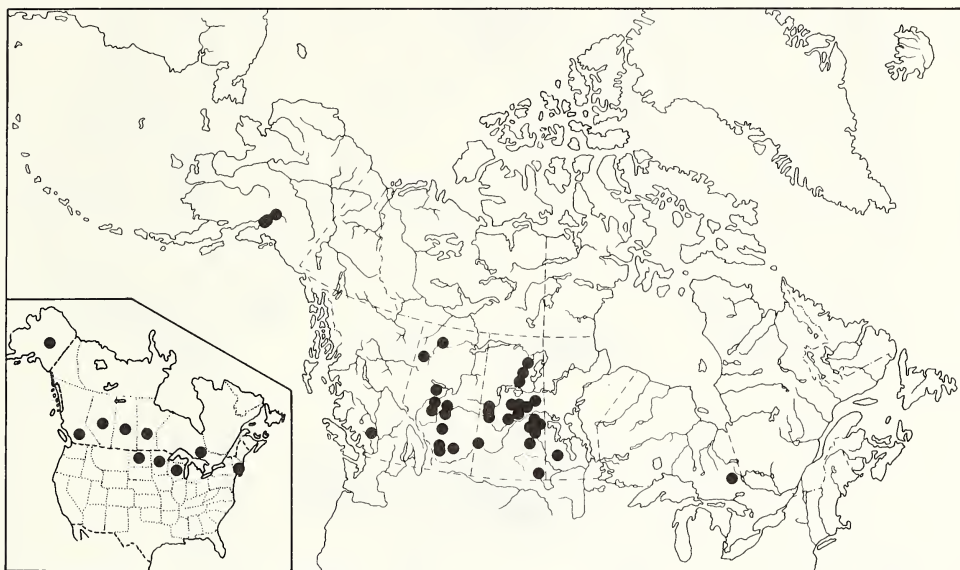
Map 68. Collection localities for *Hydropsyche riola* Denning in Canada and Alaska, with known distribution in North America by state or province.
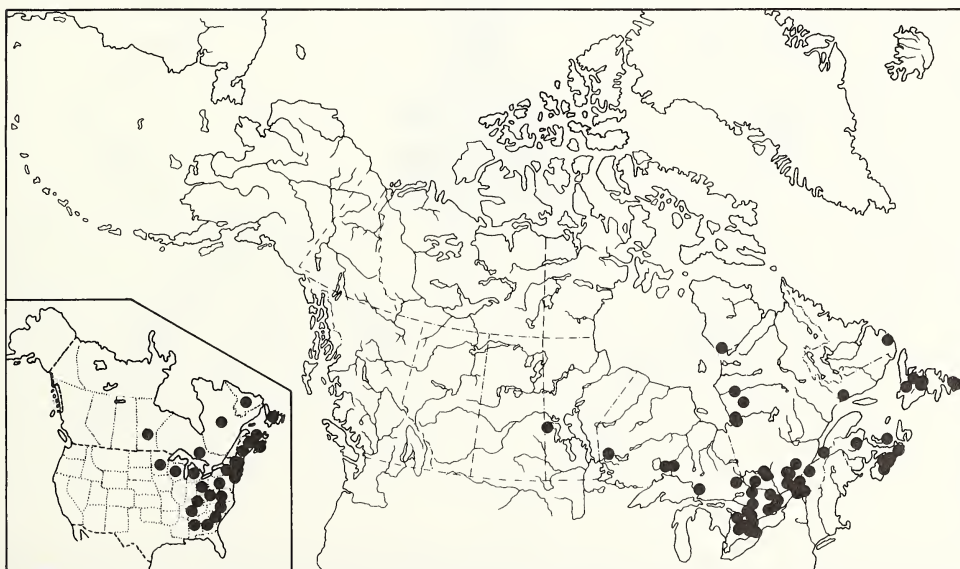
Map 69. Collection localities for *Hydropsyche sparna* Ross in Canada, with known distribution in North America by state or province.
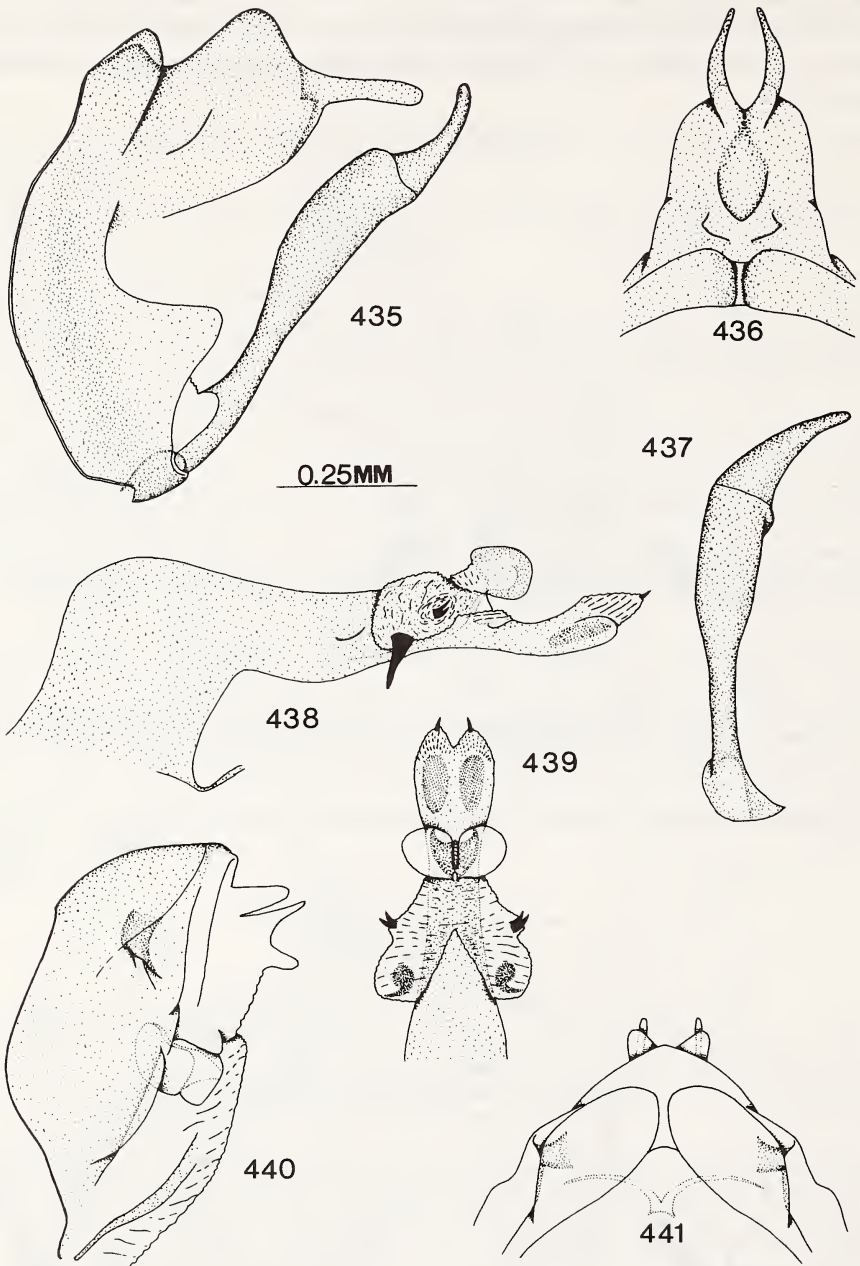
Fig. 435–441, *Hydropsyche riola* Denning: 435, genital capsule of male, lateral aspect; 436, genital capsule of male, dorsal aspect; 437, left clasper of male, posterior aspect; 438, aedeagus of male, lateral aspect; 439, aedeagus of male, dorsal aspect of tip; 440, genital segments of female, lateral aspect; 441, genital segments of female, dorsal aspect.
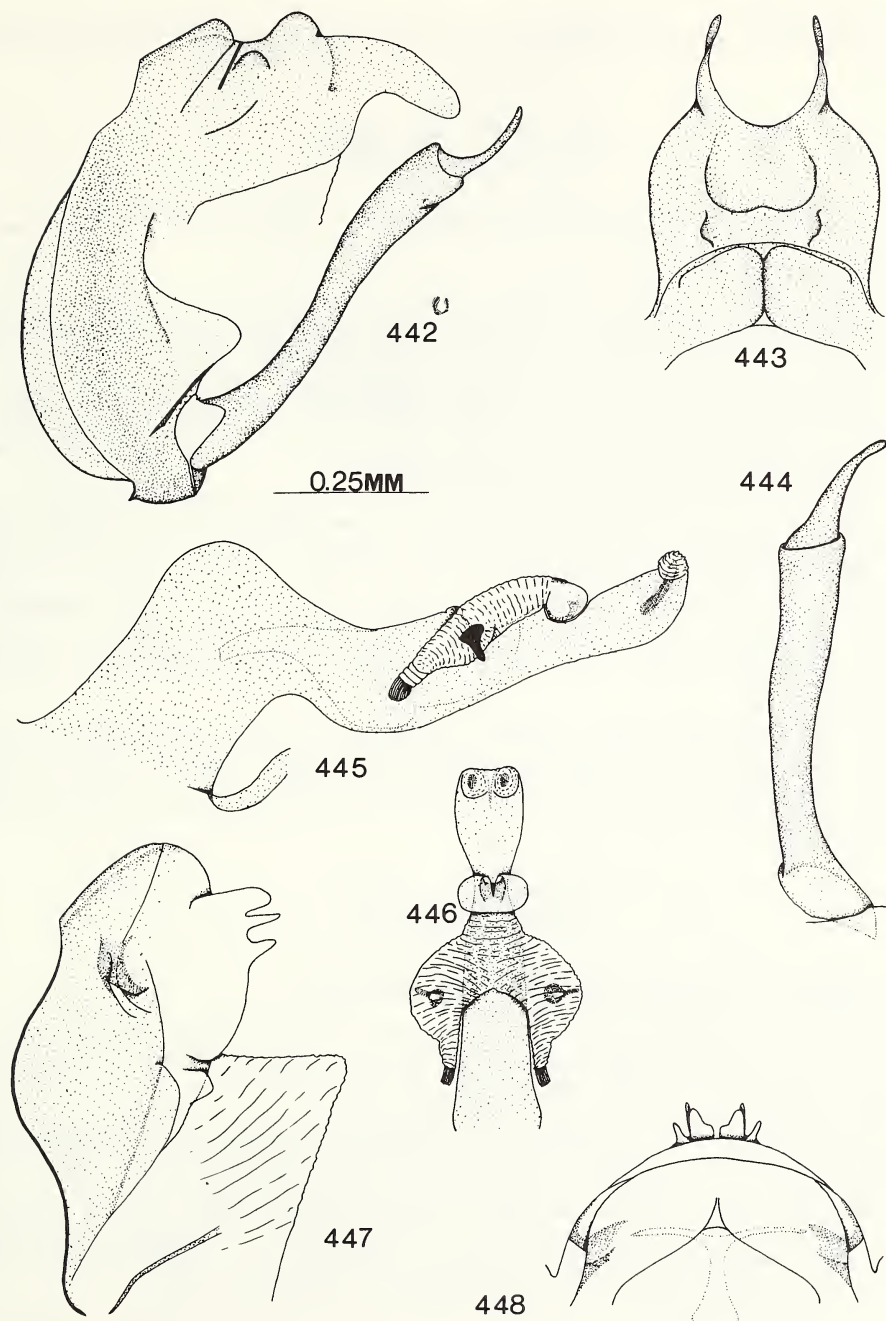
Fig. 442–448, *Hydropsyche sparna* Ross: 442, genital capsule of male, lateral aspect; 443, genital capsule of male, dorsal aspect; 444, left clasper of male, posterior aspect; 445, aedeagus of male, lateral aspect; 446, aedeagus of male, dorsal aspect of tip; 447, genital segments of female, lateral aspect; 448, genital segments of female, dorsal aspect.

SUBGROUP F

This group characterised by aedeagus dorsal membranous lobes without teeth or spines in any form.

Hydropsyche oslari Banks
Map 70; Fig. 449–455

Hydropsyche oslari Banks, 1905a:13; Betten, 1934:194; Milne, 1936:70, 71, 73; Ross, 1944:294; Schefter & Wiggins, 1986:66.
Hydropsyche partita Banks, 1914:252; Milne, 1936:73.

Description.— Male fore-wing length 9.91 mm; pale grey-brown, uniformly irrorate, with scattered larger areas of uniform colour. Antennae brownish cream; basal seven flagellar annuli each with oblique, dark band. Vertex dark brown anteriorly, to yellow-brown posteriorly. Spurs yellow to cream; lateral member of middle leg pairs notably shorter than mesal companions; not so noticeable in female. Thorax rich red-brown, to yellow-brown laterally. Legs yellowish cream.

Genitalia. Male. (Fig. 449–453). (Specimen from Oldman R., Hwy 922, Alberta). Males distinguished by distal article of clasper, in lateral aspect (Fig. 449), evenly, gradually narrowed from base to long, dorsally curved distal portion; by distal article, in posterior aspect (Fig. 451), with very long, slender, linear tip; and by dorsal lobes of aedeagus with dorsally directed median lobe between two minute lateral lobes (Fig. 452, 453).

Genitalia. Female. (Fig. 454–455). (Specimen from Oldman R., Hwy 922, Alberta). Females distinguished by clasper receptacle, in lateral aspect (Fig. 454), located high on lateral wall of segment X, directed dorso-anterad, without evident inner opening; by receptacle, in dorsal aspect (Fig. 455), directed mesad; and by vulval scale sclerotised strap long, gradually widened distally, angled at mid-point (Fig. 454).

Biology.— I have records of adults from shallow, small, rock and gravel streams of negligible turbulence, to larger rivers of swift, deep, turbulent waters (clear or turbid). Canadian flight season ranges from June 4 to September 14, with diffuse peak through July/August.

Distribution.— Western species, ranging from Mexico to western Yukon (Map 70). In Canada, widely recorded from open plains, foothills, and Boreal Forest of Alberta, from throughout British Columbia, from Vancouver Island, with one record from Dawson City, Yukon.

Hydropsyche ventura Ross
Map 71; Fig. 456–462

Hydropsyche ventura Ross, 1941:92; Ross, 1944:294; Schefter & Wiggins, 1986:80.
Symphitopsyche ventura; Schuster & Etnier, 1978:55.

Description.— Male fore-wing length 8.38 mm; uniformly very pale reddish brown; anal edge with alternate dark and pale areas. Hind-wing very palely tinted. Antennae uniform pale straw. Vertex deep red-brown, warts paler. Spurs straw-coloured. Thorax deep red-brown overall. Legs straw-coloured.

Genitalia. Male. (Fig. 456–459). (Specimen from St Hippolyte, Québec). Males distinguished by distal article of clasper, in lateral aspect (Fig. 456), of almost uniform width, with triangular tip; by tergum X distal lobes, in dorsal aspect (Fig. 457), long, slender, well spaced, curved somewhat mesad about roughly circular gap between; and by aedeagus dorsal lobes, in dorsal aspect (Fig. 460), each bilobed, with posterior short, stout lobe, and anterior long, thin lobe.

Genitalia. Female. (Fig. 461–462). (Specimen from St Hippolyte, Québec). Females distinguished by clasper receptacle, in lateral aspect (Fig. 461), oriented vertically, directed anterad, crescentic, with inner opening not visible; by receptacle, in dorsal aspect (Fig. 462), directed mesad, with inner opening on small secondary tubercle; and by vulval scale sclerotised strap with long, slender, slightly widened proximal portion, semi-circular distal portion.

Biology.— Little known. Schuster & Etnier (1978) describe one particular site in detail, but make no generalisations. They give known flight season as early April to September.

Distribution.— Recorded from Tennessee to Newfoundland, with scattered records from southern Québec, eastern Ontario (Map 71).
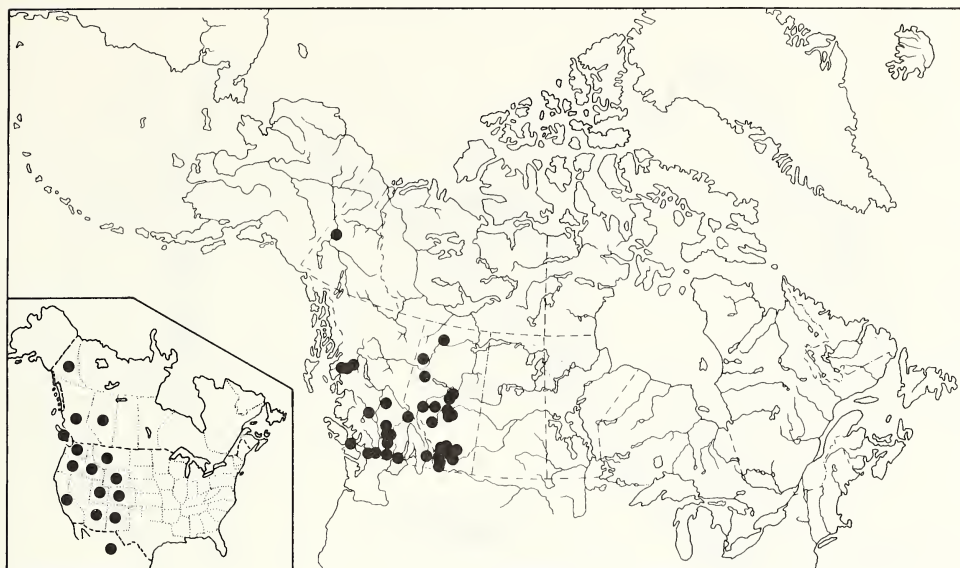
Map 70. Collection localities for *Hydropsyche oslari* Ross in Canada, with known distribution in North America by state or province.
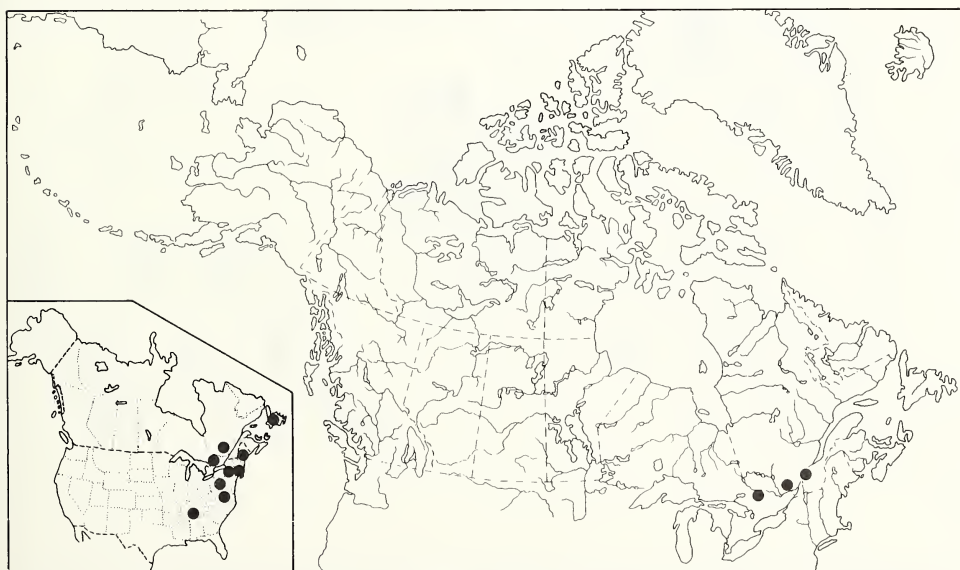
Map 71. Collection localities for *Hydropsyche ventura* Ross in Canada, with known distribution in North America by state or province.
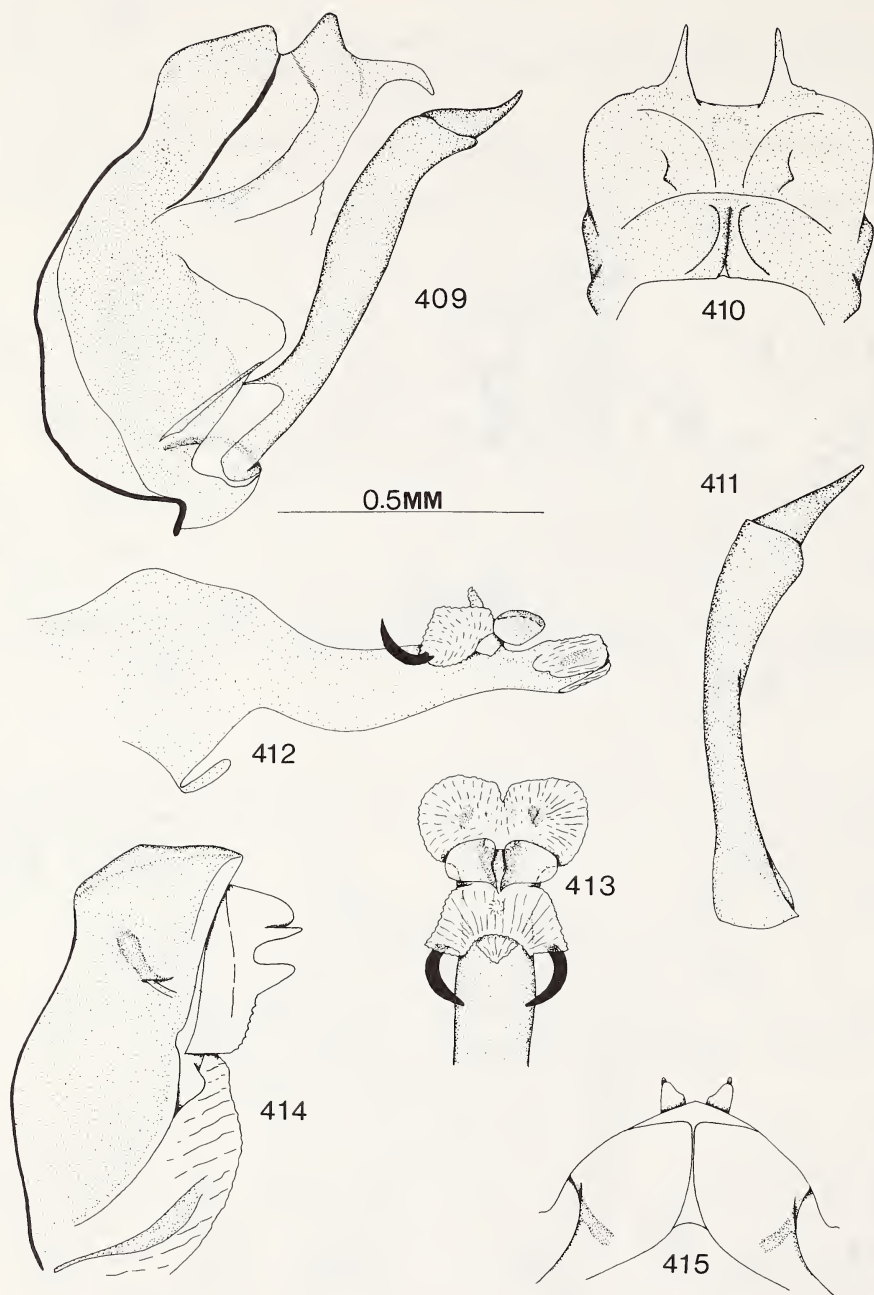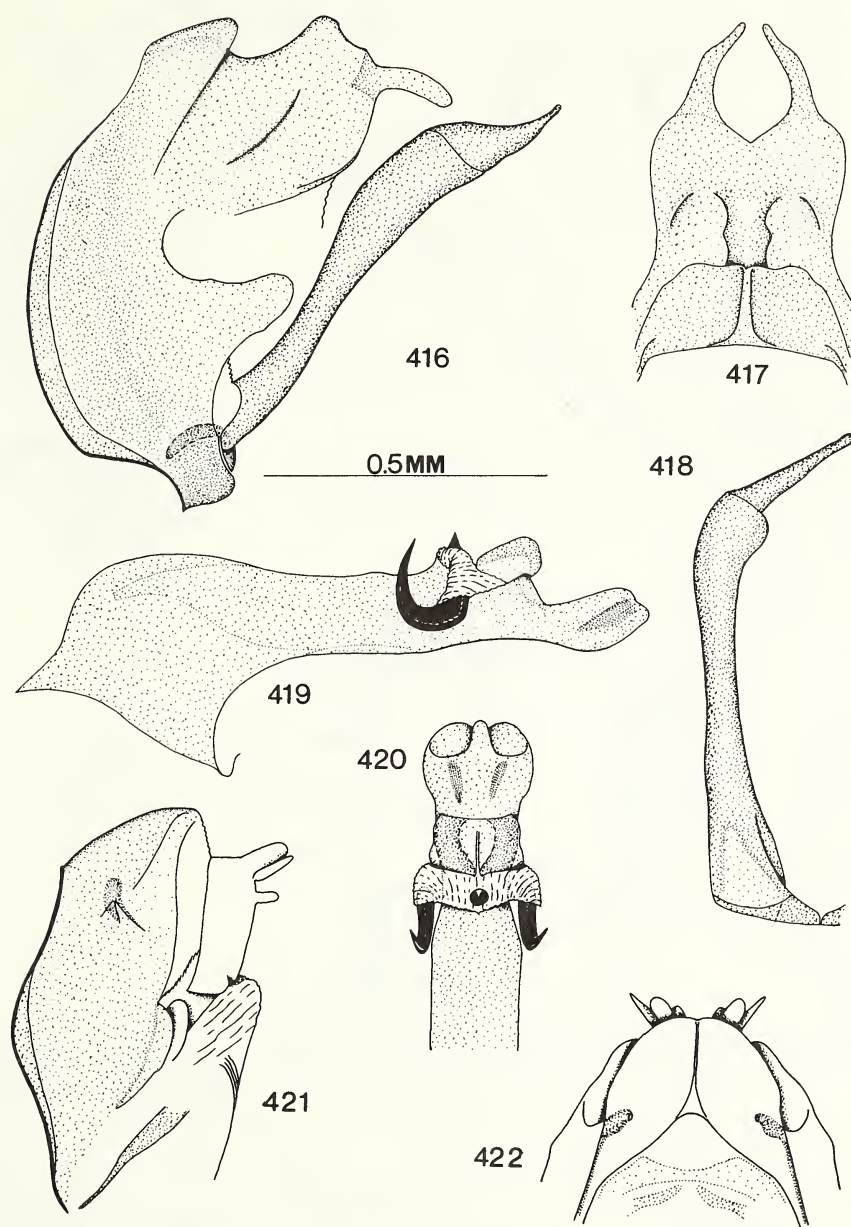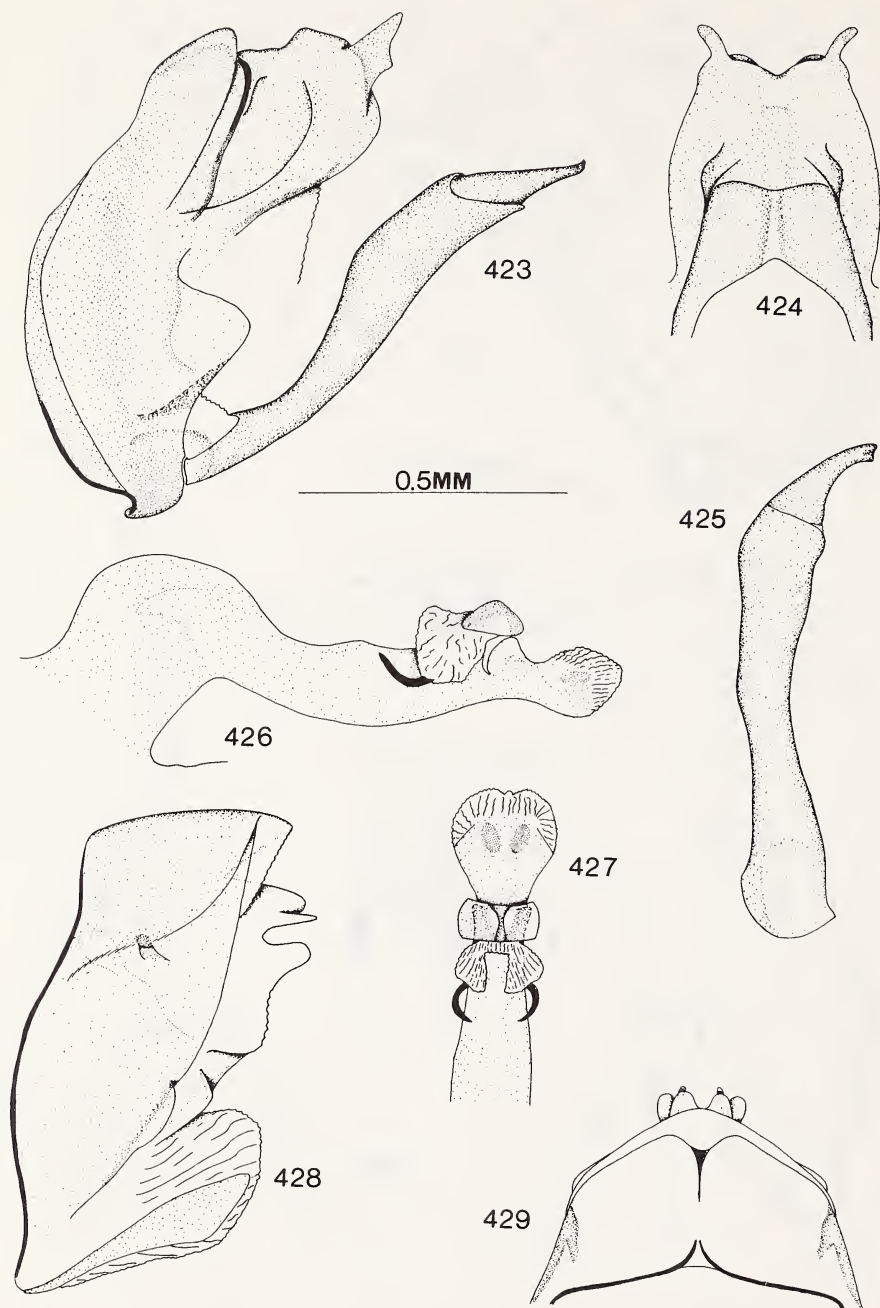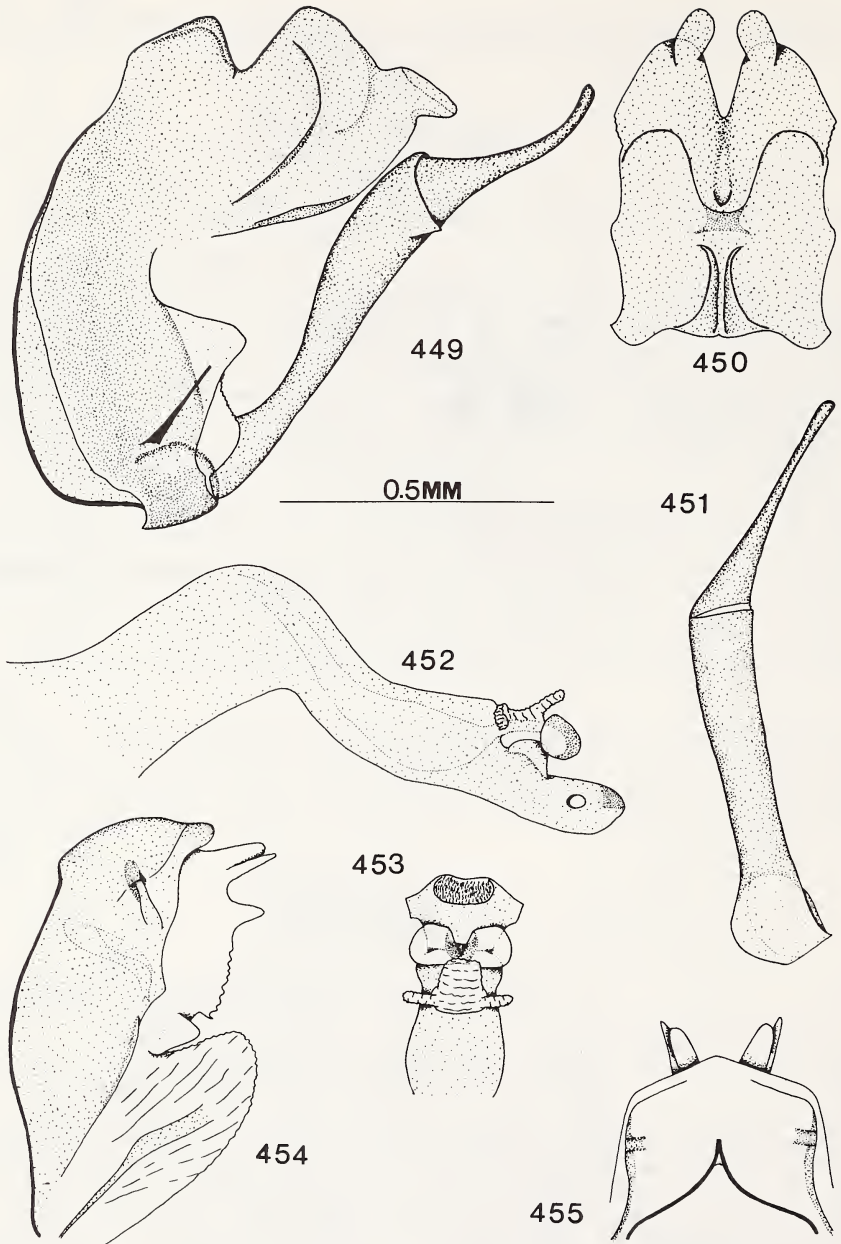
Fig. 449–455, *Hydropsyche oslari* Ross: 449, genital capsule of male, lateral aspect; 450, genital capsule of male, dorsal aspect; 451, left clasper of male, posterior aspect; 452, aedeagus of male, lateral aspect; 453, aedeagus of male, dorsal aspect of tip; 454, genital segments of female, lateral aspect; 455, genital segments of female, dorsal aspect.
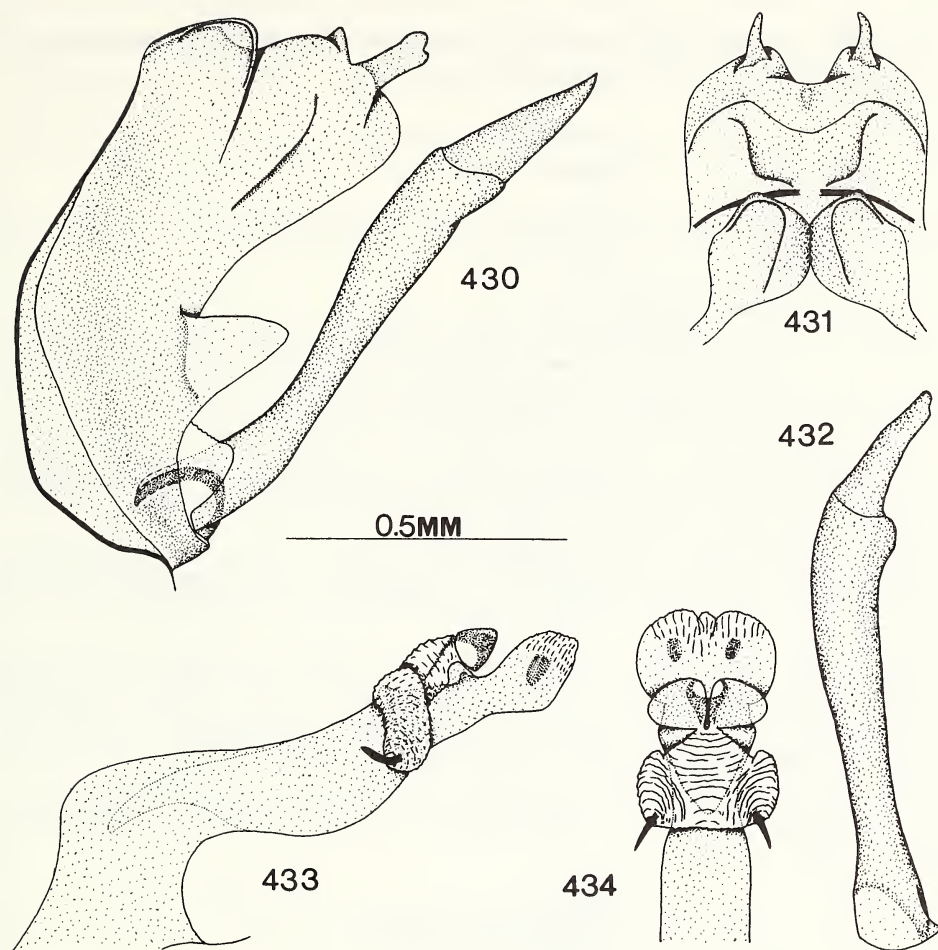
Fig. 456–462, *Hydropsyche ventura* Ross: 456, genital capsule of male, lateral aspect; 457, genital capsule of male, dorsal aspect; 458, left clasper of male, posterior aspect; 459, aedeagus of male, lateral aspect; 460, aedeagus of male, dorsal aspect of tip; 461, genital segments of female, lateral aspect; 462, genital segments of female, dorsal aspect.

Genus *Potamyia* Banks
Map 72; Fig. 6, 463–468

Potamyia Banks, 1900:259; Betten, 1934:197; Ross, 1944:85; Wiggins, 1977:116; Schmid, 1980:59.

Description.— Head globular, convex; malar space large. Antennae very fine, long, especially in male; basal article globular. Fore-wings (Fig. 6a) with few hairs. Hind-wings (Fig. 6b) large, especially in male; somewhat pointed distally. Hind-wing fl present; stems of veins M and Cu1 very close, parallel; cross-veins M3+Cu1 and Cu1-Cu2 very close together. Fore-wing without cross-veins Sc-R1 and R1-R2+R3. Spur formula 0,4,4 male; 1,4,4 female. Fore-leg tarsi of male strongly spinate; claws asymmetrical, overhung by stout, black setae.

Genitalia. Male. (Fig. 463–466). Very similar to genitalia of *Hydropsyche* and *Cheumatopsyche*.

Genitalia. Female. (Fig. 467–468). Again, very similar to genitalia of *Hydropsyche* and *Cheumatopsyche*. Sternite VIII longitudinally divided throughout. Clasper receptacle not present (Fig. 467).

The above characters are a melange of characters shared with the Macronematinae, *Hydropsyche*, and *Cheumatopsyche*, plus several peculiar to *Potamyia*.

Biology.— Larvae prefer large, warmish rivers, and appear to congregate on rocks in sandy, silt-free conditions in slower currents.

Potamyia is confined to Siberia and eastern North America east of Montana. Of two known species one, *P. flava*, is recorded from North America.

Potamyia flava (Hagen)
Map 72; Fig. 6, 463–468

Macronema flavum Hagen, 1861:285.
Potamyia flava; Banks, 1900:259; Betten, 1934:198; Denning, 1943:136; Ross, 1944:85; Wiggins, 1977:Fig. 6.11; Schmid, 1980:Fig. 141-143.
Hydropsyche flava; Milne, 1936:73.
Hydropsyche kansasensis Banks, 1905a:15; Milne, 1936:73.

Description.— Male fore-wing length 9.20 mm; uniform light brownish yellow; no pattern. Antennae light yellow-brown; basal two flagellar annuli each with oblique, paler band; less evident in female. Vertex light yellow-brown; uniform brownish yellow in female. Spurs pale, dull yellow; in female, lateral member of middle leg pairs, and hind-leg apical pair, notably shorter than mesal companions. Thorax pale, dull yellow-brown throughout. Legs dull straw; reddish yellow in female.

Genitalia. Male. (Fig. 463–466). (Specimen from Hamilton, Illinois, USA). Males distinguished by high, narrow segment IX in lateral aspect (Fig. 463); by small, acuminate, dorso-laterally directed distal lobes of tergum X (Fig. 463-466); and by distal article of clasper, in lateral aspect, widened distally.

Genitalia. Female. (Fig. 467–468). (Specimen from Washington Co., Arkansas, USA). Females distinguished by lack of any sign of clasper receptacle on lateral wall of segment X (Fig. 467); and by lack of vulval scale sclerotised strap.

Biology.— See under genus above. The only Canadian flight date is June 6, in Manitoba.

Distribution.— Widespread throughout eastern United States (Map 72), as far west as Montana; not known from New England States. In Canada Schmid (1980) reports this species from southern Ontario. I have examined material taken on the banks of the Assiniboin River, Manitoba (just W of Winnipeg).
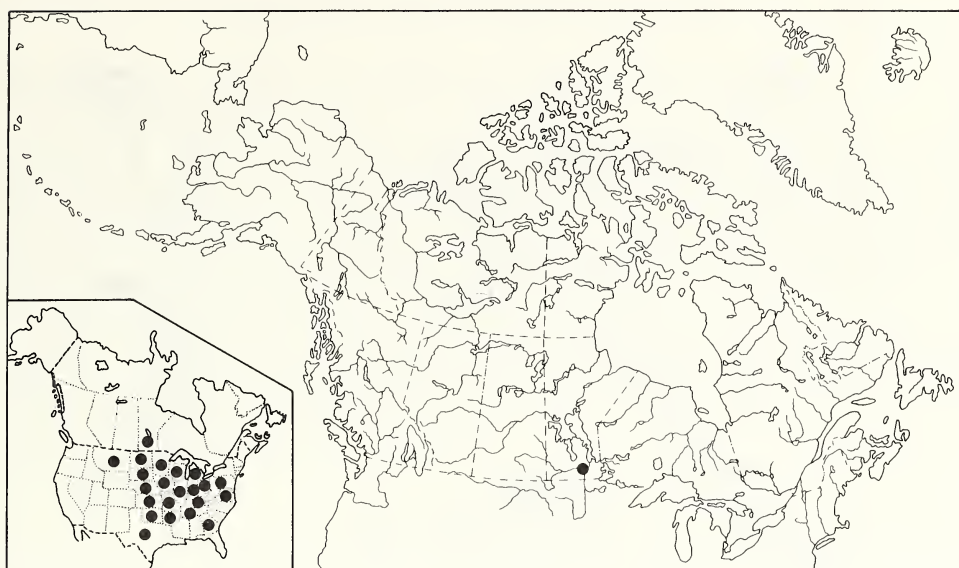
Map 72. Collection localities for *Potamyia flava* (Hagen) in Canada, with known distribution in North America by state or province.
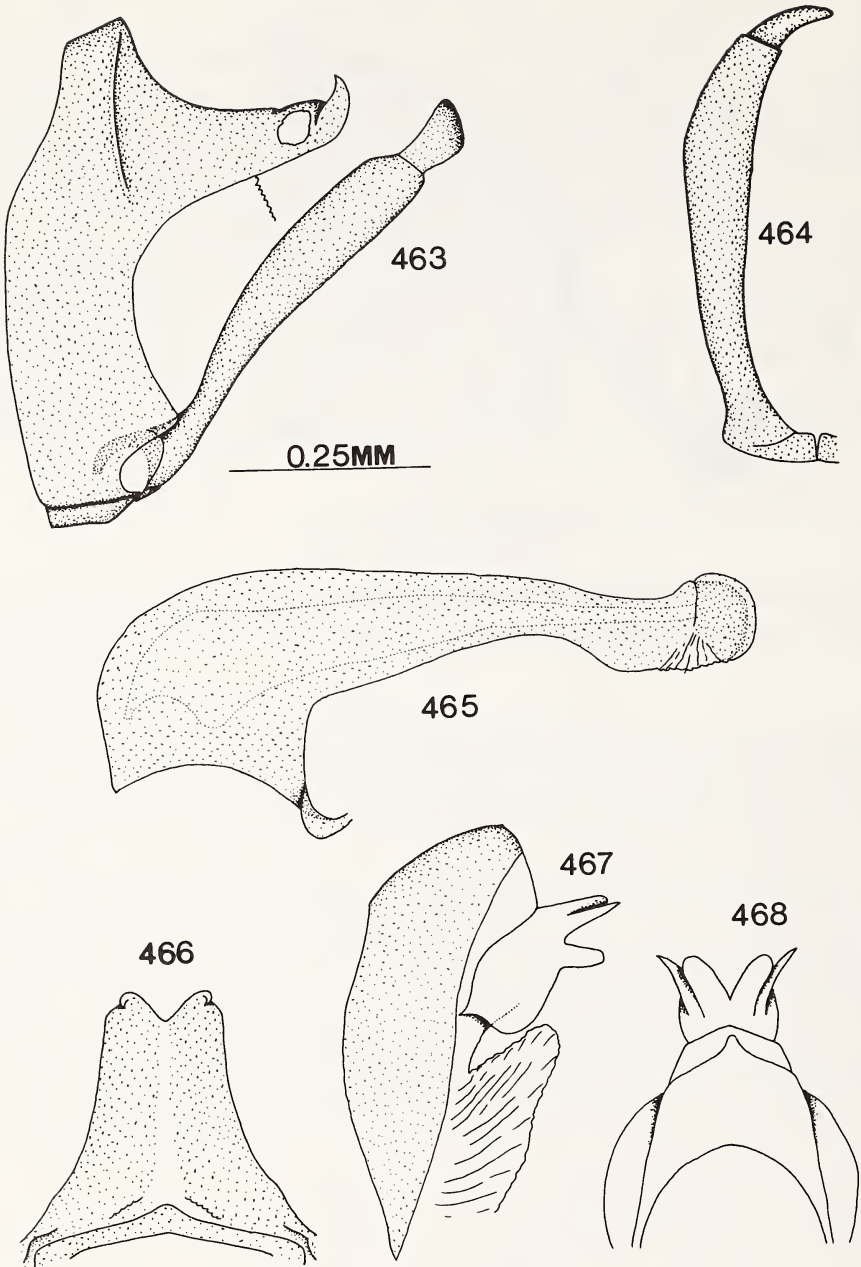
Fig. 463–468, *Potamyia flava* (Hagen): 463, genital capsule of male, lateral aspect; 464, left clasper of male, posterior aspect; 465, aedeagus of male, lateral aspect; 466, genital capsule of male, dorsal aspect; 467, genital segments of female, lateral aspect; 468, genital segments of female, dorsal aspect.

SUBFAMILY DIPLECTRONINAE ULMER

Diplectroninae Ulmer, 1951:303; Ross, 1956:10; Marlier, 1962:135; Wiggins, 1977:93; Schmid, 1980:61.

Following characterisation of adults derived from Marlier (1962).

Description.— Medium to large (wing-span 12–20 mm). Wings generally large; wide basally, rounded or angular distally. Antennae equal in length to fore-wings, or slightly longer. Cephalic warts less prominent than in Macronematinae; posterior pair large, oval; anterior pair quite small; interantennal wart round. Thorax large, robust. Male fore-leg tarsal claws normal, equal, not overhung by setal tufts. Middle leg tarsi of female not expanded, not flattened. Spur formula 2,4,4. Fore-wing Sc and R1 (Fig. 4a) complete, unfused, or joined distally; often robust. Discoidal and median cells small, subequal, closed. Forks fI-fV present; fI, fIII, and fV petiolate. Thyridial cell closed, in contact with median. Hind-wing (Fig. 4b) often widened at mid-point; Sc and R1 distinct throughout; discoidal cell closed, elongate; fII, fIII, and fV present; median cell open.

Genitalia. Male. (Fig. 469-472, 475-479). Much as usual for Hydropsychidae; simple, very little modified. Tergum X roof-like dorsad of aedeagus; not seperable from segment IX; with or without wart-like preanal appendages. Aedeagus simple (Fig. 478) or complex (Fig. 471), curved, basally expanded, without spines. Claspers (inferior appendages) long, of two articles; distal article smaller than basal article.

Genitalia. Female. (Fig. 473–474, 480-481). Much as for Hydropsychinae. With or without clasper receptacles; if present, not prominent. Cerci prominent.

Genus *Aphropsyche* Ross
Map 73; Fig. 469–474

Aphropsyche Ross, 1941:78; Ross, 1944:83.

Following generic characterisation derived from Ross (1941).

Description.— Head somewhat prognathoid; eyes widely separated, located anterad. Antennae short, somewhat robust; pedicel only half as long as scape, of thickness similar to flagellum. Vertex convex; mesal ridges inconspicuous; postero-lateral warts large. Pronotum with pair of large, close warts. Wings similar in shape, evenly rounded distally; venation generalised, typical for group; radial veins of hind-wing straight.

Genitalia. Male. (Fig. 469–472). Genital capsule basically as for Hydropsychinae, but considerably less regular in outline (Fig. 469); with postero-ventral edge produced posterad. Clasper articles not obviously distinguishable. Aedeagus complex (Fig. 471), with paired (Fig. 472), long, slender, acuminate dorsal lobes; with expanded, rounded, single ventral lobe surmounted by smaller, complex intromittent structure.

Genitalia. Female. (Fig. 473–474). Much as for Hydropsychinae. Cercus large, prominent. No clasper receptacle evident. Sternite VIII cleft mesally, more or less throughout length.

Biology.— As larvae not yet definitely associated (see Wiggins, 1977), nothing can usefully be included here.

Four species presently known: two in Asia, two in eastern North America. One is likely to be recorded in eastern Canada.

Aphropsyche doringa Milne
Map 73; Fig. 469–474

Aphropsyche doringa Milne, 1936:68-69, 73; Ross, 1944:294.
Aphropsyche aprilis Ross, 1941:78; Ross, 1944:83; Flint, 1966:374 (as synonym of *A. doringa*).

Description.— Male fore-wing length 8.81 mm; uniform purple-grey, with stigma and anal edge darker. Hind-wing uniform purple-grey. Female overall darker, more uniform in fore-wing. Antennae uniform dull brown in male; dark purple-brown in female. Vertex deep chocolate to black, warts red-brown, intense black in female with reddish black warts. Spurs purple-brown. Thorax, dorsally, as vertex in either sex; laterally, deep red-brown (to yellow-brown coxae) – deep red-brown throughout in female. Legs yellow-brown proximally, purple-brown distally; dull red-brown throughout in female.

Genitalia. Male. (Fig. 469–472). (Specimen from Reid Ck, Blount Co., Tennessee, USA). Males distinguished on basis of aedeagus alone (Fig. 471–472), with paired dorsal lobes, single ventral lobe. Other features are: clasper apparently of one article, curved gently dorsad, of uniform width except for tapered distal end; anterior edge of segment IX highly irregular in lateral aspect (Fig. 469); postero-ventral edge of segment IX with posteriorly projected shelf; and tergum X distal lobes high, black, flared postero-laterad, with slender, acuminate dorsal spine each.

Genitalia. Female. (Fig. 473–474). (Specimen from Reid Ck, Blount Co., Tennessee, USA). Females distinguished by vulval scale sclerotised, except membranous distally (Fig. 474); by anterior edge of segment X linear (Fig. 473); and by cercus large, intermediate between dorsal and ventral lobes of segment XI, with minute distal article.

Biology.— Almost unknown. Etnier & Schuster (1979) report adult occurrence in Tennessee as April 21 to May 13. Neves (1979) reports adults in Massachusetts in June.

Distribution.— Not yet known from Canada, with only scattered records from eastern United States (Map 73), from as far north as New Hampshire.
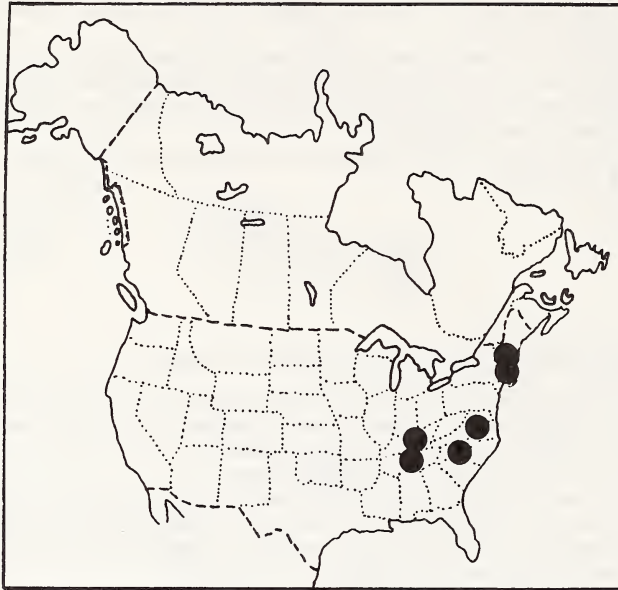
Map 73. Known distribution of *Aphropsyche doringa* Milne in North America, by state.

0.5MM
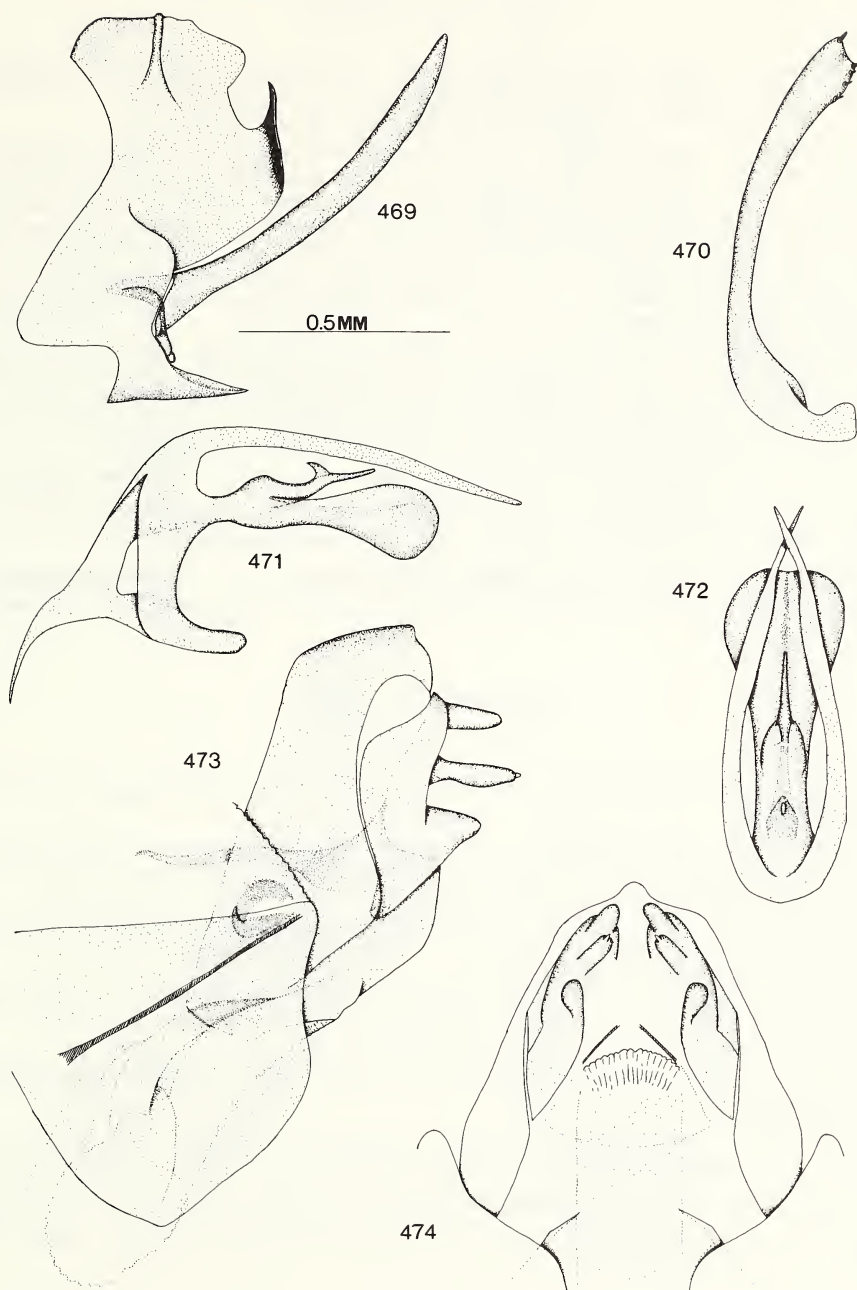
Fig. 469–474, *Aphropsyche doringa* Milne: 469, genital capsule of male, lateral aspect; 470, left clasper of male, posterior aspect; 471, aedeagus of male, lateral aspect; 472, aedeagus of male, dorsal aspect; 473, genital segments of female, lateral aspect; 474, genital segments of female, ventral aspect.

Genus *Diplectrona* Westwood
Map 74; Fig. 475–481

Diplectrona Westwood, 1840:49; McLachlan, 1978:374; Betten, 1934:182; Milne, 1936:68; Ross, 1944:84; Bull. Zool. Nomen, 1965:288 (validation: opinion 758); Wiggins, 1977:102; Schmid, 1980:61.
Aphelocheira Stephens, 1836:167, 179; Bull. Zool. Nomen., 1965:288 (suppresion: opinion 758).

Description.— Antennae as long as fore-wings, fine, notched; annuli as thick as long, swollen at mid-point; basal annuli each with oblique, dark band. Maxillary palpi with second article much longer than basal article, third and fourth articles shorter. Vertex with four large warts. Middle leg tarsi of female normal, not flattened, not enlarged. Sternite V with bulge prolonged by very long, thin tube, slightly longer in male than female. Fore-wing (Fig. 4a) widened at chord. Hind-wing (Fig. 4b) large, rounded, distally blunt. Fore-wing fI and fIII petiolate; discoidal cell small, median and thyridial cells large; Cu2 and A markedly curved, postcostal cell much enlarged; cross-veins M3+4-Cu1 and Cu1-Cu2 close. Hind-wing with Sc very thick, R1 very thin, both sinuate, subcostal cell very narrow basally, very large distally; discoidal cell narrow; fI and fIII petiolate.
Genitalia. Male. (Fig. 475–479). Segment IX without postero-lateral edge poorly developed (Fig. 475). Segment X not clearly delimited from IX, with two pairs of lobes (one mesal, the other lateral) (Fig. 476). Claspers (inferior appendages) with very long basal article. Aedeagus (Fig. 478) stout, two endothecal lobes distally (Fig. 479).
Genitalia. Female. (Fig. 480–481). Sternite VIII completely divided. Segment X with barely visible clasper receptacle (Fig. 480), produced ventrad to form distinct sclerotised strap along lateral face of vulval scale.

Biology.— Larvae found in rapid areas of small, cool streams. They have been found in moss on submerged rocks, and in leaf accumulations. Univoltine, with egg hatch in late Summer and Autumn; larvae, never abundant, mature in early summer.

Diplectrona spp. known from all regions except Ethiopian and Neotropical Regions, and Antarctic continent. Three species known in North America – two eastern, one western. One known from Canada.

Diplectrona modesta Banks
Map 74; Fig. 475–481

Diplectrona modesta Banks, 1908:266; Betten, 1934:182; Milne, 1936:68, 73; Ross, 1944:84; Wiggins, 1977:102; Schmid, 1980:Fig. 150-157.

Description.— Male fore-wing length 8.74 mm; uniform grey-brown. Hind-wings palely tinted grey-brown. Antennae red-brown. Vertex dark red-brown. Spurs brown, dark brown in female; lateral member of fore-leg pair minute relative to mesal companion; equal in female. Thorax dark red-brown, to paler laterally. Legs dark straw-brown.
Genitalia. Male. (Fig. 475–479). (Specimen from St Hippolyte, Québec). Males distinguished by distal article of clasper of uniform width, much narrower than basal article (Fig. 475, 477); by dorsum of segment IX long; and by tergum X with two pairs of lobes, in dorsal aspect (Fig. 476).
Genitalia. Female. (Fig. 480–481). (Specimen from Milton, Ontario). Females distinguished by clasper receptacle located high on lateral wall of segment X as minute, circular pit (Fig. 480); and by vulval scale sclerotised strap long, widened distally, attached to basal angle of segment X by long, irregular root.

Biology.— As above, except to add that known flight season in Canada extends from May 30 to September 26.

Distribution.— Eastern seaboard of North America from Florida to Cape Breton Island, Nova Scotia, northwest to American mid-western states and northwestern Ontario. There are records from Arkansas and Oklahoma (Map 74). In Canada, recorded from near Dryden, northwestern Ontario, to Baddeck, Cape Breton Island, Nova Scotia, south to United States border.
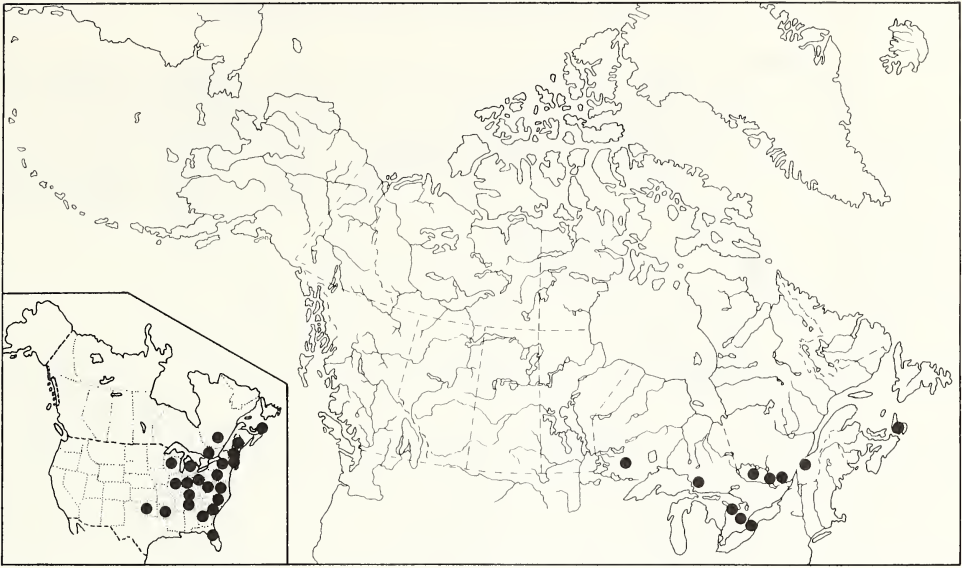
Map 74. Collection localities for *Diplectrona modesta* Banks in Canada, with known distribution in North America by state or province.
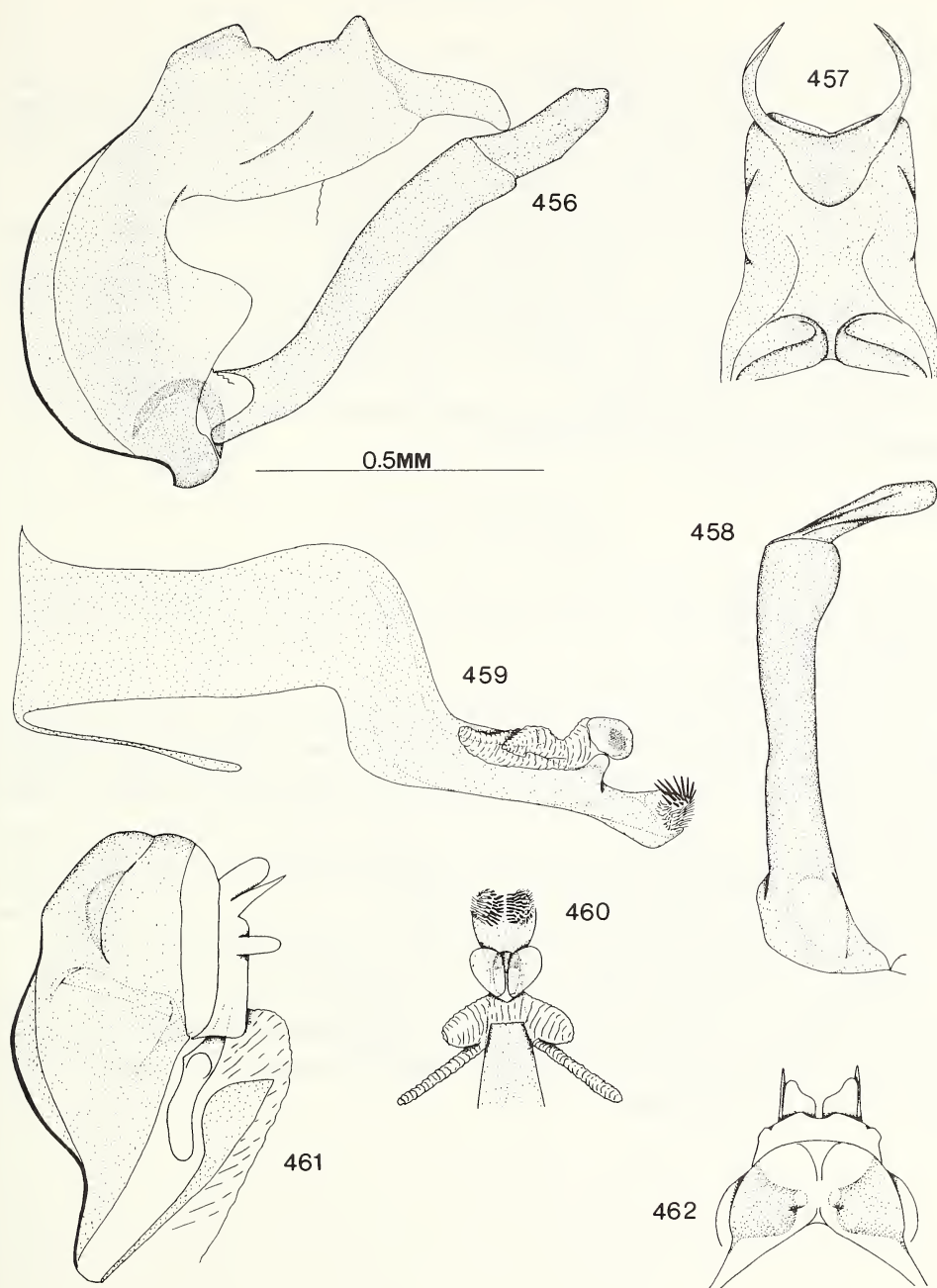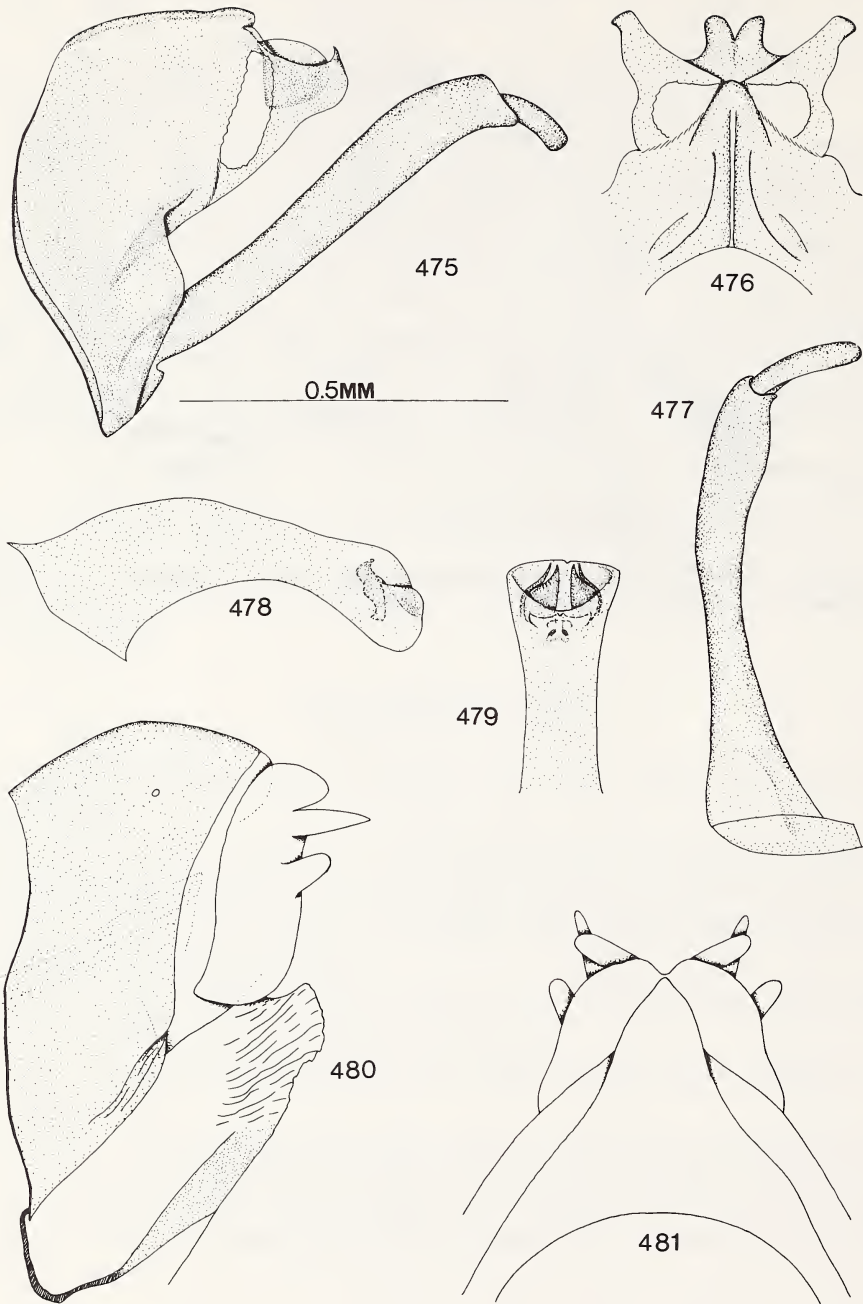
Fig. 475–481, *Diplectrona modesta* Banks: 475, genital capsule of male, lateral aspect; 476, genital capsule of male, dorsal aspect; 477, left clasper of male, posterior aspect; 478, aedeagus of male, lateral aspect; 479, aedeagus of male, dorsal aspect of tip; 480, genital segments of female, lateral aspect; 481, genital segments of female, dorsal aspect.

SUBFAMILY MACRONEMATINAE ULMER

Macronematinae Ulmer, 1905a:41; Betten, 1934:200; Milne, 1936:67; Wiggins, 1977:93; Schmid, 1980:56.
Oestropsinae Brauer, 1868. Denning, 1943:106, 155 (for Macronematinae).

As only one genus is at all likely to concern us here, the generic characterisation will suffice for purposes of this text. Those wishing full details of the subfamily should consult Betten (1934:200) and Wiggins (1977:93).

Genus *Macrostemum* Kolenati
Maps 75–77; Fig. 482–496

Macrostemum Kolenati, 1859; Flint & Bueno-Soria, 1982:358.
Macronema Pictet, 1836:400 (part); McLachlan, 1878:353 (part); Betten, 1934:203 (part); Milne, 1936:72; Denning, 1943:156 (*Macronemum*); Ross, 1944:114 (*Macronemum*); Bull. Zool. Nomen., 1962:80 (validation – opinion 623); Wiggins, 1977:110; Schmid, 1980:56.

Description.— Distinct secondary sexual dimorphism present. Head globular, vertex convex, malar space large. Antennae very fine, 1.5 times length of fore-wing, 1.3 times in female. Anterior warts of vertex very large, slightly less so in female. Maxillary palpi with two basal articles short; male flagellum 1.3 times longer than in female. Middle leg tarsi of female much enlarged, flattened. Hind-leg tibia of male with long setae. Male sternite V with finger-like lobe; minute bump in female. Wings sparsely hirsute; fore- and hind-wings of different shapes; fore-wing slenderly elliptical; hind-wing triangular, 1.5 times size of fore-wing, not so large in females; female hind-wing with distinct costal angle. Hind-wing venation somewhat irregular, incomplete. Fore-wing Sc and R1 joined prior to distal edge; fI-fV present, fI petiolate; discoidal, median cells small, thyridial cell very long, postcostal cell very large; A1 very long. Only fII, fIII, and fV present in hind-wing; R1 and R2+3 joined with Sc; discoidal cell open; M with origin at base of RS. Fore-wing variously banded transversely with light and dark colour.
Genitalia. Male. (Fig. 483–487, 490–494). Segment IX, in lateral aspect (Fig. 490), elongate; short dorsally and ventrally. Segment X comprised of two large lobes (Fig. 491), produced postero-laterad; meso-internal area membranous. Claspers (inferior appendages) long, of more or less uniform thickness, of two subequal articles. Aedeagus fairly stout basally, greatly swollen distally, simple (Fig. 493, 494).
Genitalia. Female. (Fig. 488–489, 496). Sternite VIII cleft twice on posterior edge, to form three lobes, or once to form two lobes (Fig. 489). Segment X roughly triangular in lateral aspect (Fig. 488, 496); ventral angle produced, vulval scale enclosed. Segment XI slightly developed; normal two papillate lobes of hydropsychids slender, distinct; space between lobes occupied by several smaller, papillate, membranous processes. Cerci small, of two articles.

Biology.— Larvae inhabit larger rivers, and ingest fine particulate detritus, phytoplankton, and bacteria.

Macrostemum is a widespread genus, found in Africa, Asia, Australia, with three species known from eastern North America.

Key to known or potential species of *Macrostemum* Kolenati of Canada

1a	Wings pale yellow, with narrow, transverse brown stripes (more diffuse in female) . . . . *M. transversum* (Walker), p. 174	
1b	Wings with longitudinal stripes (purplish brown) on basal part, transverse stripes distad of these, with irregular patch of brown on distal quarter of wing (more diffuse in females, with smaller patches of brown) 2	
2a	(1b)	Compound eye large relative to head in lateral aspect (Fig. 482), vertex low . . . . *M. carolina* (Banks), p. 174
2b		Compound eye small relative to head in lateral aspect (Fig. 495), vertex high . . . . *M. zebratum* (Hagen), p. 174

Macrostemum carolina (Banks)
Map 75; Fig. 482

Macronema carolina Banks, 1909:342; Betten, 1934:204; Milne, 1936:73, 74; Ross, 1944:116 (*Macronemum*).
Macrostemum carolina; Flint & Bueno-Soria, 1982:369.

Description.— Male fore-wing length 10.06 mm; purplish brown with large areas of yellow-brown disposed in longitudinal bars (basal) or transverse bars (mid-way to tip), with irregular patch in distal quarter. Female pattern more diffuse; dark areas paler distally, with distal quarter almost all pale yellow-brown. Hind-wing translucent pale brown, almost hyaline along costal edge. Antennae dark reddish brown. Vertex dark purplish brown. Spurs yellowish brown; lateral member of middle leg pairs, and hind-leg apical pair, notably shorter than mesal companions. Thorax virtually black, to very deep purplish brown laterally. Legs brown to yellow. Eyes large relative to head, malar space below not wide, rather narrow (Fig. 482). Vertex low in lateral aspect – this point will separate *M. carolina* from *M. zebratum*.

Genitalia. Male. (Not illustrated – identical to those of *M. zebratum*). (Specimen from Washington Co., Arkansas, USA). *M. carolina* and *M. zebratum* may be separated from *M. transversum* by segment IX and tergum X with membranous partial gap between, in lateral aspect (Fig. 490); and by tergum X distal lobes, in dorsal aspect (Fig. 491), with mesal edges parallel, gap between u-shaped.

Genitalia. Female. (Not illustrated – identical to those of *M. zebratum*). (Specimen from Washington Co., Arkansas, USA). *M. carolina* and *M. zebratum* may be distinguished from *M. transversum* by bases of cerci and lobes of segment XI enclosed laterally by postero-lateral edge of segment X; and by segment X wide from top to bottom (Fig. 496).

Biology.— South Carolina flight season is May to September. Wallace & Scherberger (1974) discuss larval retreat and net in detail.

Distribution.— Not yet recognised from Canada. In United States, recorded from most states from Oklahoma east to Florida, Illinois, and New York (Map 75).

Macrostemum transversum (Walker)
Map 76; Fig. 483–489

Hydropsyche transversa Walker, 1852:114
Macronema transversum; McLachlan, 1866:264; Betten, 1934:205; Milne, 1936:72, 74; Ross, 1944:117 (*Macronemum*); Kimmins & Denning, 1951:120.
Macrostemum transversum; Flint & Bueno-Soria, 1982:369.
Macronema polygrammatum McLachlan, 1871:129; Betten, 1934:204, 205 (*M. polygrammaticum*); Kimmins & Denning, 1951:106 (as synonym of *M. transversum*).

Description.— Male fore-wing length 12.95 mm; pale yellow-brown with deep red-brown patches and bars; distal area of yellow-brown as transverse bar. Female fore-wing with dark patches more diffuse; distal transverse bar less distinct, extended to costal edge of wing. Hind-wing hyaline. Antennae pale orange-brown. Vertex very wide, short; deep red-brown, warts paler. Spurs yellow; lateral member of all pairs shorter than mesal companions; most noticeable on middle leg. Thorax deep red-brown throughout; venter clothed in long, very fine, hyaline pubescence. Legs straw-coloured; clothed in long, very fine, hyaline hairs.

Genitalia. Male. (Fig. 483–489). (Specimen from Altahana R., Appling Co., Georgia, USA). Males distinguished by pattern of sinuate, branched lines on segment IX and tergum X in lateral aspect (Fig. 483); by tergum X distal lobes, in dorsal aspect, separated by v-shaped gap (Fig. 484); and by no distinct division between segment XI and tergum X.

Genitalia. Female. (Fig. 488–489). (Specimen from Altahana R., Appling Co., Georgia, USA). Females distinguished by cerci and segment XI lobes entirely posterad of any overlap by lateral wall of segment X (Fig. 488); and by segment X narrow from top to bottom, in lateral aspect.

Biology.— No flight season data available. Wallace & Sherberger (1975) provide a detailed account of larval retreat and feeding net.

Distribution.— Not yet known from Canada. United States records scattered (Map 76), including Washington D.C., Virginia, Georgia, Indiana, and Ohio.

Macrostemum zebratum (Hagen)
Map 77; Fig. 490–496

Macronema zebratum Hagen, 1861:285; Betten, 1934:205; Milne, 1936:72, 74; Denning, 1943:157; Ross, 1944:115 (*Macronemum*); Wiggins, 1977:110; Schmid, 1980:Fig. 124-130.

Macrostemum zebratum; Flint & Bueno-Soria, 1982:369.

Phryganea (Leptocerus) hieroglyphica Harris – *nom. nud.*, invalid; Hagen, 1873:297 (as synonym of *Macronema zebratum*).

Phryganea (Leptocerus) variegata Harris – *nom. nud.*, invalid; Hagen, 1873:297 (as synonym of *Macronema zebratum*).

Description.— Identical to *M. carolina* (see *M. carolina* above). May be distinguished from *M. carolina* by eyes small relative to head (Fig. 495), malar space small, vertex high in lateral aspect. Also, *M. zebratum* is larger species, with fore-wing length of male 14.04 mm.

Genitalia. Male. (Fig. 490–494). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Identical to *M. carolina.*

Genitalia. Female. (Fig. 496). (Specimen from Ile Ste Héléne, St Lawrence R., Montréal, Québec). Identical to *M. carolina.*

Biology.— Wallace (1975) reports on larval feeding, and net structure. Larvae inhabit rivers from large to very largest, found primarily in rapids. Canadian flight season ranges from June 1 to September 8.

Distribution.— Other than a curious record from Utah, this species is confined to eastern North America (Map 77), east of line from North Dakota to Georgia. Recorded northeastward to Maine. In Canada, abundantly recorded from southern Québec and Ontario, with one isolated record from Ignace, far northwestern Ontario.
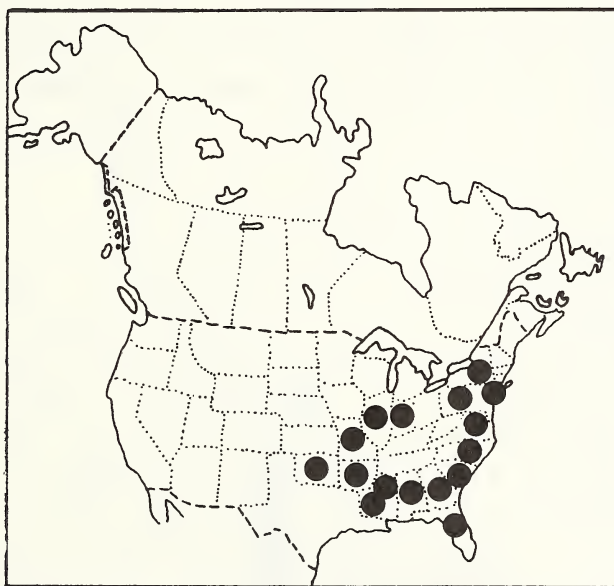
Map 75. Known distribution of *Macrostemum carolina* (Banks) in North America, by state.

Map 76. Known distribution of *Macrostemum transversum* (Walker) in North America, by state.
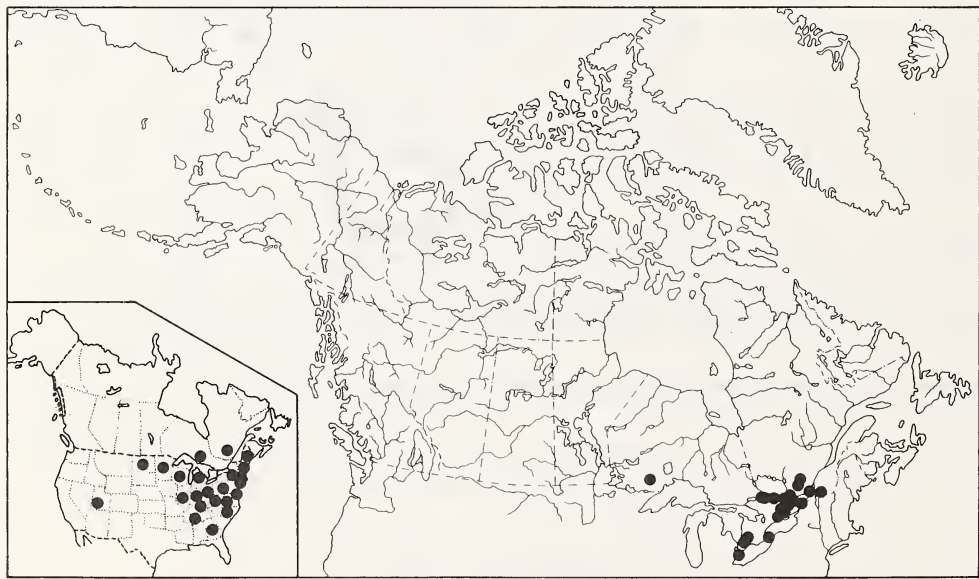
Map 77. Collection localities for *Macrostemum zebratum* (Hagen) in Canada, with known distribution in North America by state or province.
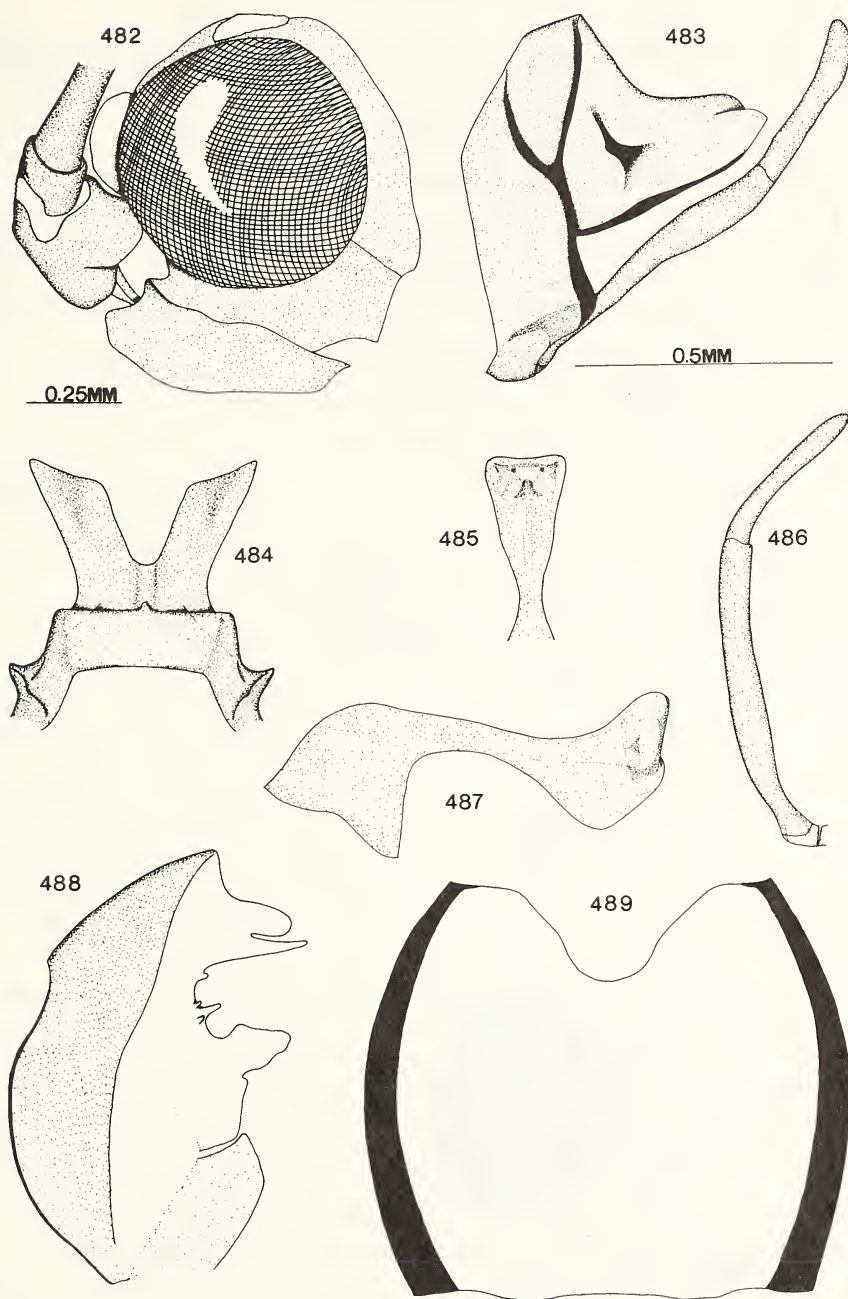
Fig. 482–489. 482, *Macrostemum carolina* (Banks): head of male, lateral aspect. 483–489, *Macrostemum transversum* (Walker): 483, genital capsule of male, lateral aspect; 484, genital capsule of male, dorsal aspect; 485, aedeagus of male, dorsal aspect of tip; 486, left clasper of male, posterior aspect; 487, aedeagus of male, lateral aspect; 488, genital segments of female, lateral aspect; 489, sternite VIII of females, ventral aspect.
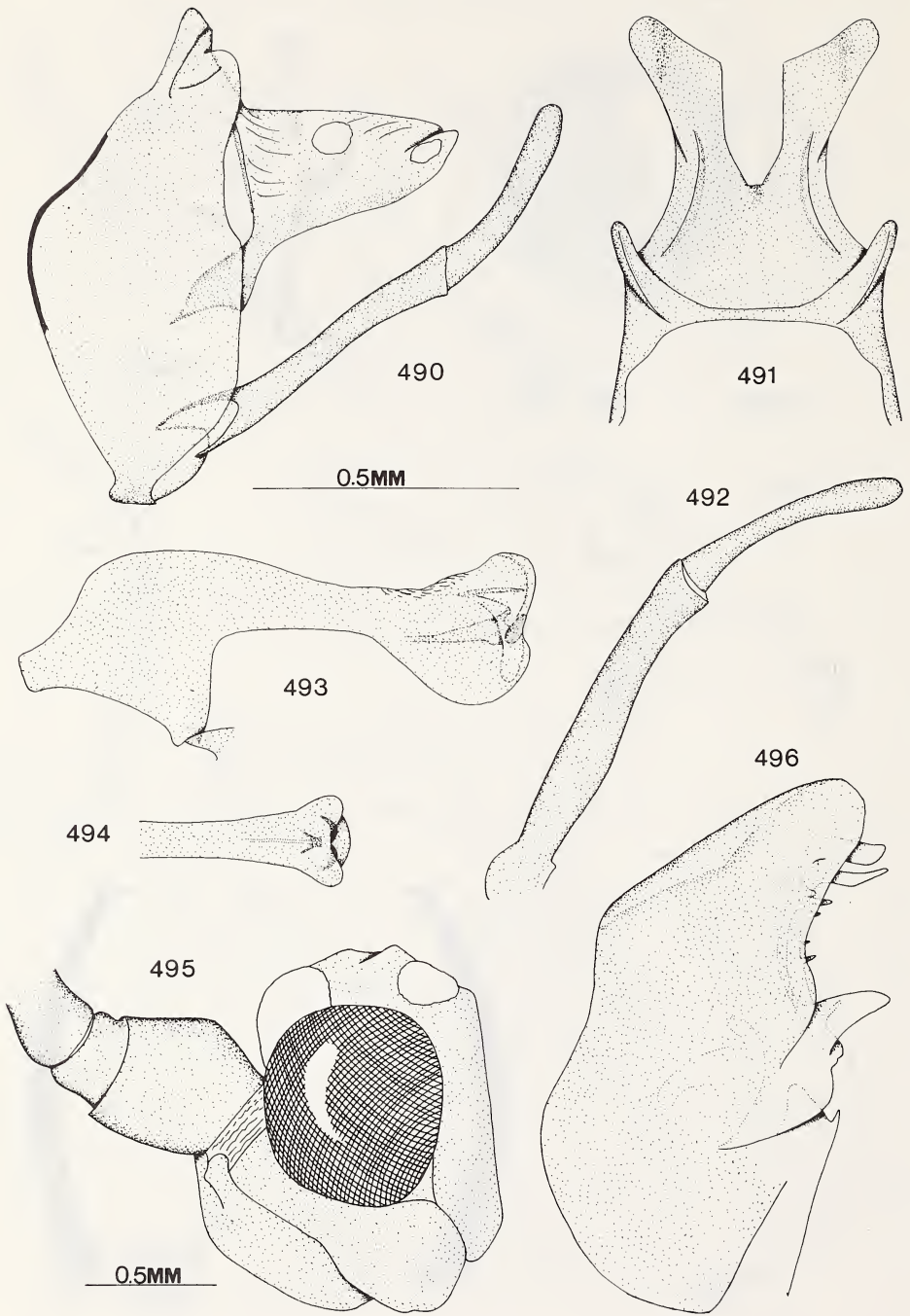
Fig. 490–496, *Macrostemum zebratum* (Hagen): 490, genital capsule of male, lateral aspect; 491, genital capsule of male, dorsal aspect; 492, left clasper of male, posterior aspect; 493, aedeagus of male, lateral aspect; 494, aedeagus of male, dorsal aspect of tip; 495, head of adult male, lateral aspect; 496, genital segments of female, lateral aspect.

ACKNOWLEDGEMENTS

And finally, in the hope that it is unneccesary, I apologise to anyone not acknowledged here, who should have been.

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(Synonyms in italics)

BOOK REVIEW

Campos-Ortega, J. A. and V. Hartenstein. 1985. The Embryonic Development of *Drosophila melanogaster*. Springer-Verlag. Berlin, Heidelberg, New York,Tokyo. 227 pp., 85 figs., 2 tables, subject index. $120.00Can.

Flies of the species *Drosophila melanogaster* are arguably the best understood of all higher animals because of their enormous popularity with geneticists since 1909 when T. H. Morgan first started culturing them in his "fly room" at Columbia University. To-day they are the organisms of choice for legions of highly ingenious and pecunious developmental biologists interested in understanding how genes control cell determination and differentiation in higher animals.

In the last decade, a flood of papers have appeared on the genetic basis of cell determination and pattern formation in *Drosophila* embryos--most recently on the mode-of-action of genes controlling segmentation of the germ band (segmentaion genes) and longitudinal specification of segment identity (homoeotic genes). Most of these papers have been based on use of genetic dissection methods and have involved analysis of mutant embryonic and larval phenotypes (more recently, use of recombinant DNA and immunocytochemical techniques has predominated). However, in spite of this explosion in experimental results, the standard description of normal embryogenesis against which they are compared has remained Sonnenblick's and Poulson's superb but now out-of-date chapters in Demerec's (1950) *Biology of Drosophila* (updated but with little added by Fullilove and Jacobson [1978] and Bownes [1982]). Campos-Ortega and Hartenstein's new book supplants these classic accounts with style and depth (it is dedicated to Donald F. Poulson).

Eggs of *D. melanogaster* average 0.42 x 0.15 mm and require about one day to develop from fertilization to hatching at 25°C. This development is described in great detail in the eight chapters of this book. Chapter 1 (6 pp.) presents a brief, illustrated (12 drawings), summary of embryogenesis in this species and chapter 2 (75 pp.) a system for staging it. The authors divide embryogenesis into 17 stages ranging in length from 10 min (each of stages 6 and 7) to 11.7 hr (stage 17) and summarize the events occurring in each stage. These events are illustrated with 71 photomicrographs of living whole mounts and 123 of fixed embryos embedded in plastic and sectioned longitudinally or horizontally.

Origin and differentiation of most organ systems are considered in Chapter 3 (79 pp.) – including the gut, Malpighian tubules, salivary glands, gonads, somatic and visceral musculature, dorsal vessel, fat body, epidermis, central (CNS), peripheral (PNS) and stomatogastric (SNS) nervous systems and the tracheal system. The chapter is illustrated with 42 drawings, 56 photomicrographs and seven transmission electron micrographs – the most impressive of the drawings being Fig. 3.14 (a lateral view of a first instar larva with every external cuticular structure illustrated), Figs. 3.23-3.25 (detailed, 3-dimensional reconstructions of all external sensilla and their projections to specific ganglia of the CNS in both ventral and lateral aspect), and Fig. 3.30 (six 3-dimensional reconstructions illustrating neurogenesis of the CNS). (The origin and differentiation of the CNS is remarkably similar to that recently described in great detail in various grasshopper embryos by Goodman, Bate and their colleagues).

The pattern of embryonic cell division is summarized in Chapter 4 (7 pp., 6 drawings) and is shown to occur during two periods. The first takes place prior to cell formation at blastoderm and involves 13 rounds of mitosis. The first seven zygotic divisions are synchronous and yield a

syncytium of 128 nuclei distributed as an ellipsoid within the yolk. With the next 3 mitoses (8-10), the resulting nuclei approach the peripheral periplasm to form the syncytial blastoderm with 200 nuclei remaining behind in the yolk as vitellophags and 17-18 entering the posterior pole plasm to form pole cells (germ line cells). Three further (11-13) and now parasynchronous mitoses increase the number of syncytial blastoderm nuclei to about 5000 at which time cell membranes form between adjacent nuclei. During the second period of mitosis, from blastoderm formation to hatching, most cells divide only two or three more times - exceptions being the teloblastic nerve mother cells (neuroblasts) of the CNS, sensillar stem cells and pole cells.

Chapter 5 (13 pp., 16 drawings) considers the morphogenetic movements involved in changing the simple cellular monolayer of the blastoderm into the complex, 3-dimensional structure of the young embryo. These movements occur either by growth and infolding of certain regions of the blastoderm or by movement of cells or groups of cells into the interior and can involve cell proliferation, changes in cell shape and size, and shifting of individual cells in relation to each other. Gastrulation, germ band elongation and (later) shortening, head involution and dorsal closure are among the more important of these movements in *Drosophila* embryogenesis. With gastrulation, 1250 cells invaginate from the ventral midline of the embryo to form mesoderm and endoderm leaving 3750 cells about the yolk to form the rest of the larval body (ectoderm). The germ band elongates 220% around the posterior end of the egg during germ ban elongation and later, during its shortening, each thoracic and abdominal segment shortens and broadens – a shape change attained through shape changes of their individual cells.

Cephalogenesis (Chapter 6-13 pp., 9 drawings, 11 photomicrographs) includes head involution, a phenomenon unique to higher Diptera (Cyclorrhapha). At stage 11, the developing head is similar to, though less complex than, heads of other insect embryos at comparable stages of development and contains a large procephalon and three gnathal segments each bearing a pair of short, blunt, appendages. Portions of all these segments shift cephalad during the remainder of embryogenesis and invaginate into the front of the embryo to form the atrium of the foregut in which is later secreted the cuticle of the larval cephalopharyngeal skeleton. The segmental source of the various parts of this skeleton are indicated (the mouth hooks, for example, derive from the maxillary appendages).

Certain aspects of segmentation are considered in more detail in Chapter 7 (12 pp., 8 drawings, 2 tables) including formation of segmental borders, epidermal sensory organs, muscle innervation, and homologies between the muscles and sense organs of each segment.

The final chapter (8- 8 pp., 2 drawings) presents a new fate map of the *Drosophila* blastoderm. This was derived by use of three methods: 1. The enzyme horse radish peroxidase (HRP) was injected into donor eggs before cellularization. This tracer spreads freely throughout each embryo and becomes incorporated into all its cells during cellularization. Just after cellularization, labelled cells are taken from these donors by means of a micropipette and transplanted singly into unlabelled host embryos. The progeny of each transplanted cell is then traced during subsequent development of the host embryo. 2. Progressively older embryos were removed from their choria and vitelline membranes and stained with fuchsin (every nucleus can be counted and drawn in such embryos) 3. Planimetric reconstructions of complete series of sections of embryos of similar age were prepared by "rolling off" folded and invaginated tissues. Use of these methods enabled the authors to obtain reliable quantitative data for each embryonic stage. Fig. 1B illustrates this fate map for one side of the blastoderm and indicates

the number of blastoderm cells contributing to each larval organ derived from that side (for example, 150 blastoderm cells give rise to one half the proctodeum). The rest of this chapter considers cell number in each organ and the number of blastoderm cells giving rise to it.

Production quality of the book is outstanding, for paper, printing and binding, and the halftones of the photomicrographs are of uniformly high standard. This last was because all sections were cut from eggs dechorionated and fixed according to Zalokar and Erk's (1977) phase-partition method (which causes essentially no disruption of egg contents) and embedded in plastic. There are a few typographical errors and some awkward grammar but not much, considering that the senior author is Spanish and the junior author German. My principal criticisms are its outrageous price, the total absence of scanning electron micrographs (available from the work of Turner and Mahowald [1976–1979] and cited in the book), and the almost total absence of reference to embryos of other insects (only Goodman *et al*'s work on grasshopper neurogenesis, Anderson's (1962, 1972) synopses, and Wheeler's (1891, 1983) and Weisman's (1863) classical descriptive studies are mentioned). Their discussion of head segmentation in chapter 6, for example, would have been vastly improved had they referred to Rempel's (1975 Quaest. Ent. 11: 7-25) critical review of this topic. (This subject has recently been considered at great length for this species by Jürgens *et al.*, Rous's Archives of Developmental Biology 195: 359–377. [1986]). There are only 112 references.

However, this book was written for *Drosophila* workers--not for comparative embryologists or entomologists--and as such will be indispensible to all individuals investigating the embryos of these insects (most recent papers cite it). There are no descriptive studies of the embryos of other insects that even approach this study in detail, and it is now the standard of excellence against which all future such investigations will be compared.

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BOOK REVIEW: INSECTS FOR ALL SEASONS

TAUBER, M.J., C.A. TAUBER AND S. MASAKI. 1986. *Seasonal Adaptations of Insects.* Oxford University Press, New York. 411 pages, 16 text figures, bibliography, author index, species index, subject index. Price $39.95 USA.

When I consider writing up an investigation somewhat removed from the area of my most recent endeavor, I begin by reading a book that reviews the general topic. I have two main objectives: (1) to increase confidence about my grasp of the literature, and (2) to help forge a more synthetic entomological backbone for the paper that I would like to write. With these goals in mind, I purchased *Seasonal Adaptations of Insects* off the shelf in Blackwell's Bookstore, despite its scandalous British price. The book did not offer immediate help with either of my objectives, but instead laid bare the breadth of my ignorance about an important and interesting field of entomological research. The treatment is well organized and solidly documented with meaty discussions of work relevant to all major groups of insects. It is an excellent synthetic synopsis of a complex literature that has grown by leaps and bounds during the past 15 years. The authors lead the reader to delight in, rather than despair over, the incredible variety of phenological adaptations in insects, and suggest the outlines for a more holistic approach to empirical studies of insect life cycles. After reading the book, I share the authors' enthusiastic optimism about the future of such work. I also think that I got my money's worth!

The first five chapters provide a basis for understanding seasonal adaptations in the context of the "diapause syndrome". Chapter 1 provides a brief but useful historical summary about work on insect life cycles and clearly focuses the reader on the authors' two main objectives: (1) to describe the variety of seasonal adaptations employed by insects, and (2) to provide a synthetic basis for ecological and evolutionary studies of diapause. Chapter 2 provides a classification of the ways that insects respond to seasonal change and places diapause within a broader adaptive context. Chapter 3 describes the course of diapause with reference to the endless variations known among insects.

The fourth chapter is the keystone of the book, laying out the authors' concept of diapause. Their "diapause syndrome" is a more global and dynamic concept than those that are generally employed, and I found it more satisfying. For Tauber, Tauber and Masaki, diapause is not primarily concerned with surviving adverse conditions, but instead, with effecting broadly adaptive synchrony between insect population dynamics and seasonal variation in the environment, both biotic and abiotic. In their view then, the anticipatory nature of diapause is paramount, and seasonal synchronization is linked explicitly to neurohormonal bases. This broad concept removes any possible confusion between dormancy and diapause, isolates the evolution and development of cold hardiness as a parallel problem, and incorporates dormancy, migration and various polymorphisms in the adaptive context of the entire life cycle.

Chapter 5 is a brief but effective summary of how environment regulates seasonal cycles. Evidence for the central position of photoperiod in many species is crisply summarized, the primary inductive and secondary modifying effects of temperature are discussed, and these are considered in relation to other environmental characteristics known to influence the manifestation of diapause. The basis for constructing photoperiod response curves and for the concept of critical photoperiod are critically reviewed. Although the authors show that substantial progress has been made by assessing responses to static photoperiods, they argue that we must adopt a more dynamic approach in order to get crucial information about

diapause intensity, and in order to understand the effects of changing daylengths experienced by natural populations. The chapter is an excellent guide to the important primary literature, and work about groups that I know well was efficiently and accurately abstracted.

In Chapter 6, the authors explicitly tackle the vast diversity of insect life cycles by extending the general principles summarized in the first part of the book to insects of highly specialized adaptive zones or extreme habitats. The section about parasitoids underscores the diverse range of ways that the insect-parasitoid relationship can affect the life cycles of either partner. We also learn about how the unique aspects of social life are tied up in regulation of phenology among the social Hymenoptera. Unfortunately, there is only a passing descriptive reference to one paper about termites, and uncharacteristically, the authors do not mention whether more extensive information is available. The treatment of diapause in tropical insects is fascinating. Two important points are well established: (1) numerous tropical species show diapause, and (2) diapause is clearly adaptive in at least some tropical populations and not simply a result of introgression from more temperate populations. The chapter concludes with treatments of phenology in desert and arctic insects. Diapause is an important component of life in such environments and the diapause syndrome of arctic and desert species has been molded in weird and wonderous ways. However, as the authors point out, we have much to learn about the details of insect life cycles in both environments.

Chapters 7–9 consider the diapause syndrome as an evolutionary phenomenon. In Chapter 7, the authors partition genetic variation for seasonal adaptation into continuous variation in quantitative traits and disjunct variation in qualitative traits. They offer solid arguments about the fitness implications of quantitative traits such as intrapopulation variation of critical photoperiod, but also show that some variation has little direct relation to fitness and may have little adaptive value. They provide general guidelines for working out the genetics of diapause and document them with reviews of information now available. It appears that most quantitative traits are under polygenic control with genetic diversity maintained by variable selection pressures and intrapopulation genetic exchange. The relative importance of particular diversity maintaining processes are still a matter of dispute and may likely vary among taxa. Although Mendelian inheritance has been shown in only a few insect taxa where seasonal traits vary discretely, the authors believe that this will become more common as more detailed studies are made. The authors also discuss how genetic variation in polygenic traits can lead to polymorphisms with the incorporation of a threshold mechanism allowing continuous variation to be expressed discretely. This chapter provides a good starting place for anyone contemplating an evolutionary study of insect life cycles.

Chapter 8 provides an evolutionary scenario for diapause that links the diverse seasonal adaptations summarized in the earlier chapters and explains their control by a host of seasonal token stimuli. This general model allows for the obvious multiple evolution of diapause in the context of three steps. First, the authors assume the evolution of a time measuring system of some sort. The authors review the several models that have been published and show that there is still more to learn before we can make an informed choice among them. Second, their scenario requires the evolution of environmentally controlled neuroendocrinological responses in an adaptive context. The third stage involves the coupling of the neuroendocrine responses to seasonal environmental stimuli. The authors go on to show how their scheme provides a useful way of thinking about the evidence for evolution of diapause that has accumulated from studies employing artificial selection, work about colonizing species, and a host of comparative studies. In an illuminating critical discussion, they outline the benefits and limitations of the sorts of

broad comparative studies that have been made, and finish with a plea for detailed comparisons of environmental and physiological control mechanisms in groups of related species with well established phylogenies. This approach can reveal the polarity of diapause evolution in specific lineages. A simple, but yet instructive example is provided by discussion of the Taubers' own work with green lacewings in the *Chrysopa carnea* species complex.

The general evolution of life histories is viewed in the context of seasonal adaption in Chapter 9. Up to now most studies of insect life history have considered isolated features or suites of characters that are obviously co-adapted. Their diapause syndrome concept underscores that adaptation to seasonality influences life cycle timing and many other features of insect life history, and the authors rightly urge us to take a broader view of life history evolution in insects. Two important proximate objectives are readily accessible. First, we need to understand the limits of genetic variation for life history traits and relate the pattern of such variation to environmental correlates such as are envisioned by Southwood's (1977, *J. Anim. Ecol.* 46:337–365) notion of the "habitat templet". Genetic variation for life history has obvious geographical correlates and these are outlined in the context of a few well reviewed studies. Geographical variation in life cycles may also be related to speciation in many taxa. Second, we can search for pattern in how life history traits evolve together in the context of seasonality with particular attention to how fitness tradeoffs are managed by natural selection. Life cycles are indeed adaptive, but they are also constrained by their underlying genetic systems. We need to know more about how variation for life history traits is maintained before we can make progress toward this objective. The final chapter effectively discharges the entomologist's standard social obligation by showing how understanding of life cycles is crucial to pest management. It is largely a summary of current applications and a discussion of several approaches that are under development now. There is not much new information or conceptual synthesis useful to pest managers. However, for those desiring a summary of the anthorpo-centric justification for studying insect life cycles, the chapter will be useful. It is ideal reading for intoductory students in pest management and I will use it in my own teaching.

The book may be criticized because it largely ignores developments in the trendy literature of life history evolution. However, such criticism would miss the point. The authors and most entomologists are compelled by both interest and practical necessity to explain both highly complex life cycles and more life history variation than fits comfortably into general theoretical frameworks that have been developed to date. This book clearly establishes that life history variation within insect species, and often within populations, is as important as general patterns at higher taxonomic levels. Understanding how such variation is maintained and distributed geographically and taxonomically can become a major unifying theme in future work about insect life history.

The book is carefully written and produced. It is admirable for its clarity and scarcity of typographical error. Each chapter section is clearly summarized and this is very handy for both preview and review. The bibliography is immense, including nearly 2000 entries, most of which are cited in constructive arguments in the text. The indicies are superb and will make the book valuable as a reference on any entomological bookshelf. *Seasonal Adaptions of Insects* is a perfect basis for graduate seminar courses, and for allowing professional entomologists to catch up on an exploding literature.

Although the book confronts complexity squarely and without apology, the organization and presentation of material makes it easily digestible. Of the two objectives mentioned in the introductory chapter, the authors clearly succeed with the first; the complexities of insect life

history are superbly described and well documented. They light the way for an assault on the second objective by urging researchers to consider the genetic basis of insect life history, and to view life history in the more holistic context of the diapause syndrome. It is fair to point out that this task was begun by collections of authors at the last few International Congresses of Entomology [Dingle, H. (ed.), 1978, *Evolution of Insect Migragion and Diapause*, Springer-Verlag; Brown, V.K. and I. Hodek (eds.), 1983, *Diapause and Life Cycle Strategies in Insects*. Junk]. However, Tauber, Tauber and Masaki's new book is the first attempt to review the relations between insect life history and seasonality within a general entomological framework. Their book is highly successful and entomologists of all persuasions will profit from reading it. I hope that it will be widely read, and trust that it will inspire attention to the many fascinating problems that it raises.

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Quaestiones

Entomologicae

A periodical record of entomological investigations,
published at the Department of Entomology,
University of Alberta, Edmonton, Canada.

CONTENTS

EVOLUTION OF THE *PAPILIO MACHAON* SPECIES GROUP IN WESTERN CANADA (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT

Three species of the Papilio machaon group live in western Canada: P. machaon, P. zelicaon *and* P. polyxenes. *Most specimens of these three species are distinguished on the basis of morphological, electrophoretic or ecological characters. However, all three species hybridize along zones of parapatry, as well as in restricted areas within regions of sympatry.*

All populations of the species group whose larvae eat Artemisia dracunculus *are considered subspecies of* P. machaon. *Also* P. machaon pikei *(type locality: Dunvegan, Alberta) is described as a new subspecies from the Peace River region of northern Alberta and British Columbia.* P. m. avinoffi *and* P. kahli *are considered different expressions of hybridization between* P. machaon *and* P. polyxenes, *while* P. nitra *is treated as a genetically integrated morph within* P. zelicaon.

Three separate principal components analyses (PCAs), on 10 electrophoretic loci, 11 wing and body color characters, and the combined data set, respectively, gave very similar relative distributions of individuals and populations. Hybrid populations had intermediate mean character values, but much broader ranges of variation than those of the parental species. Enzyme genotypes were tested for conformance to Hardy-Weinberg proportions, with the same loci showing major interruptions in gene flow in some regions, but not in areas where hybrid swarms had formed. Discriminant function analyses of specimens reared on different foodplants supported the conclusions based on PCAs, and gave better species separations in some regions.

The P. machaon *group includes a wide variety of populations associated with different foodplant, habitat and climate conditions. The genetic versatility of the group leads either to ecological divergence between populations, or to localized genetic merging. Large interspecific hybrid populations have formed in central and southern Alberta* (P. zelicaon X machaon) *and in central Manitoba* (P. polyxenes X machaon), *and show varying amounts of ecological isolation from the parental species. On the other hand,* P. m. pikei *is a grassland race which was probably derived early in the Holocene from arctic/alpine populations of* P. machaon. *Hybrid swarm formation predated habitat alteration by European settlers in central Alberta, but may have been a more recent and agriculturally related phenomenon in central Manitoba. Both* P. zelicaon *and* P. machaon *also show introgression of a black wing morph from* P. polyxenes. *This morph has moved far beyond the range of* P. polyxenes, *and such specimens show electrophoretic and ecological characteristics identical to those of the populations of* P. zelicaon *and* P. machaon *in which they are now found.*

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In general, allopatric differentiation and peripheral race formation appear to account for most of the systematic structure of the P. machaon *group, though gene exchange between species is also an important factor. The presence of a widespread but uneven pattern of gene flow among the species of the* P. machaon *group necessitates a loose application of current species concepts, and causes considerable uncertainty in phylogenetic reconstructions.*

Comparison of features of the P. machaon *species group with those of potential sister groups in the genus* Papilio *indicates that color pattern of the ancestral stock of the former was probably like that of* P. machaon *itself, and that the larvae were probably umbellifer-feeders. The* P. machaon *group contains* P. alexanor, *which has problematical, though basal, affinities to the remaining four lineages (1,* P. machaon *+ hospiton; 2,* P. zelicaon; 3, P. polyxenes *+ joanae + brevicauda; and 4,* P. indra). *The Holarctic* P. machaon *lineage is older than the other three, which are Nearctic in distribution. Relationships of the latter three lineages to one another are unclear, and their divergence is represented as a trichotomy. Calculation of Nei's genetic distance suggests that* P. machaon, P. zelicaon *and* P. polyxenes *arose in Pliocene time.*

North America was invaded via *Beringia by the ancestral stock of the* P. machaon *group and, during Pleistocene time, by* P. machaon *itself. Environmental changes, particularly glaciation, caused several periods of range expansion and retraction. Differentiation in isolation led to shifts in ecological features, such as larval foodplants, as well as morphological features and electromorph frequencies. Subsequent contact led to genetic introgression and hybridization, depending in part on the extent to which isolates had diverged ecologically. These events are reflected in western Canada in the genetic structure and relationships of: three species; five subspecies of* P. machaon; *two combinations of hybrid swarms; and evidence of introgression, particularly of genes for black wing morphs.*

RÉSUMÉ

Trois espèces du groupe Papilio machaon *sont retrouvées dans l'Ouest Canadien:* P. machaon, P. zelicaon and P. polyxenes. *La plus part des spécimens de ces trois espèces se distinguent sur la base de charactères morphologiques, électrophorétiques et écologiques. Toutefois, des individus hybrides de ces trois espèces sont retrouvés aux abords des zones parapatriques, ainsi que dans des endroits restreints à l'intérieur des régions sympatriques.*

Toutes les populations de l'espèce groupe Artemisia dracunculus *dont les larves se nourrissent, sont considérées comme sous-espèces de* P. machaon. *Une nouvelle espèce,* P. machaon pikei *(localité type: Dunvegan, Alberta) est décrite pour la région de Peace River, au nord de l'Alberta et de la Colombie-Britanique.* P. m. avinoffi *et* P. kahli *sont considérés comme différentes expressions de l'hybridation de* P. machaon *et* P. polyxenes, *tandis que* P. nitra *est considéré comme un morphotype génétiquement intégré à* P. zelicaon.

Trois différentes Analyses en Composantes Principales (ACPs) effectuées respectivement sur 10 loci électrophorétiques, 11 caractères basés sur la couleur des ailes et du corps, et sur un groupe combiné de ces caractères, ont produit des distributions relatives très similaires pour les populations et les individus. Les populations hybrides démontrent des caractères moyens de valeurs intermédiaires, mais possèdent des variations bien supérieures à celle des espèces parentales.

Les enzymes génotypiques son testés pour conformité aux proportions de Hardy-Weiberg, utilisant les même loci démontrant une interruption majeure du courant d'échange génétique de quelques régions, mais non dans les régions où les essaims hybrides se sont formés. Une analyse en fonctions discriminantes utilisant les spécimens écimens élevés sur différentes source de nouriture, supportent les conclusions basées sur les A.C.P., et démontre pour quelques regions une meilleure séparation des espèces.

Le groupe P. machaon *inclut une grande variété de populations associées à différentes sources alimentaires végétales, habitats et conditions climatiques. La versatilité génétique du groupe conduit soit à une divergeance écologique, soit à des combinaisons génétiques localisées. De larges populations hybrides se sont formées dans le centre et le sud de l'Alberta (*P. zelicaon X machaon*) et dans le Maitoba central (*P. polyxenes X machaon*). Ces populations démontrent différents degrés d'isolation écologique de leurs espèces parentales. Toutefois,* P.m. pikei *considéré comme une espèce des prairies, a probablement évolué au début de l'Holocène, d'une population arctique/alpine de* P. machaon. *La formation d'essaims hybrides dans l'Alberta centrale, précède la période d'altération de l'habitat induite par l'établissement des*

colons Européens; mais est probablement plus récente et reliée à l'agriculture dans le Manitoba central. P. zelicaon ainsi que P. machaon démontrent l'intégration d'un morphotype à aile noire provenant de l'espèce P. polyxenes. Ce type s'est réparti bien au delà de l'aire de distribution de P. polyxenes, et de tels spécimens démontrent des charactères électrophorétiques et écologiques identiques à ceux des populations de P. zelicaon et P. machaon dans lesquelles ils sont maintenant retrouvés.

De façon générale, la différenciation allopatrique et la formation de races périfériques semblent être responsable d'une grande portion de la structure phylogénétique du groupe P. machaon, bien que l'échange génétique interspécifique soit aussi un facteur important. La présence d'un courant d'échanges génétiques largement répendu, mais irrégulié, entre les espèces du groupe P. machaon nécessite une utilisation au sens large du concept d'espèces, et de ce fait induit de considérables incertitudes lors de la reconstitution phylogénétique.

La comparaison des traits charactéristiques du groupe-espèce P. machaon à ceux de potentiels groupes-soeurs dans le genre Papilio, indique le patron de couleurs de la souche ancestrale était probablement comme celui de P, machaon lui-même, et que les larves se nourissaient probablement de plantes umbellifères. L'espèce P. alexanor, qui fait parti du groupe P. machaon, a des rapports fondamentaux mais problématiques aux quatres autres lignées (1, P. machaon + hospiton; 2, P. zelicaon; 3, P. polyxenes + joanae + brevicauda; and 4, P. indra). Parmi les quatres lignées, la lignée Holarctique P. machaon est plus ancienne que les trois autres qui sont de distribution Nearctique. Les rapports entre les trois lignées néarctiques sont ambigus et ainsi la divergence est décrite en trichotomie. Le calcul de distance de Nei semble indiquer que P. machaon, P. zelicaon et P. polyxenes proviennent de l'âge Pliocène.

L'amérique du nord a été envahie via le Beringia par la souche ancestrale du groupe P. machaon et durant l'âge Pleistocène par P. machaon lui-même. Des changements d'environnement en particulier la glaciation, ont causé plusieurs periodes d'expansion et de rétraction de distribution. Les différences d'isolement ont mené aux changements de caractères écologiques tels que plantes-hôtes des larves autant que caractères morphologiques et fréquences d'electomorphs. Le contact subséquent a mené à l'introgression et à l'hybridisation, selon le degré de divergence écologique des isolées. Ces évennements se sont réflechis dans l'ouest du Canada par la structure génétique et les rapports entre trois espèces; cinq sous-espèces de P. machaon, deux combinaisons de deux essaims hybrides; et l'évidence d'introgression, en particulier les gènes pour les morphs aux ailes noires.

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INTRODUCTION

The genus *Papilio* traditionally includes 30 to 40 species groups, of which the *Papilio machaon* L. group is one. Adults of the group are predominantly black and yellow (Plates 1–3), and are relatively large (forewing length: 3.5 to 5.0 cm). The *P. machaon* group is principally defined by larval characters, especially a color pattern of black segmental bands and by use of hostplants in the families Umbelliferae or Compositae.

Opinions about the number of species included within the *P. machaon* group range from four (Eller, 1939) to between 10 and 20 species (*e.g.,* Remington, 1968a). Eight species are

recognized in this study, and three of them are dealt with in detail. There is much less difference of opinion about the limits of the group itself, with most recent authors following Monroe (1961).

Most of the uncertainty about the number of species which should be recognized within the *P. machaon* group is caused by discordant character variation. For example, *P. machaon* and *P. hospiton* Géné remain distinct and easy to distinguish where they contact each other on Corsica and Sardinia, but *P. machaon* has races in North Africa and the Arabian peninsula which are much more similar to *P. hospiton* (Clarke and Larsen, 1986). Wing and body color pattern, and wing shape, have been the main morphometric characters used to distinguish among *P. machaon* group species. However, for identifications of *P. machaon*, *P. zelicaon* Lucas and *P. polyxenes* Fabricius, no one character is completely dependable. Most diagnoses list several characters, and there has been no effort published previously to quantify rigorously these differences using multivariate techniques. The presence of several color polymorphisms within populations has also been a consistent source of taxonomic confusion. The most notable example is the adult morph with black wings, whose features are probably determined by homologous alleles in different species.

Other kinds of taxonomic characters have shown only limited utility. Differences in male genitalia, which are taxonomically valuable in many groups in the Papilionidae, are of minor importance in the *P. machaon* group. In North America adults of only one species, *Papilio indra* Reakirt, can be consistently distinguished on this basis. Use of chromosomal characters (Maeki and Remington, 1960; Maeki, 1976; Clarke *et al.*, 1977) involves substantial technical difficulties. Although gel electrophoresis has been useful for elucidating systematic relationships in many taxa, there have been no reports about variation of enzyme alleles in the *P. machaon* group.

The *P. machaon* species group has a holarctic distribution. It occurs throughout North America and in higher elevations as far south as Peru and Venezuela. It also ranges across Eurasia, southward to South China and North Africa. The group is represented in virtually any vegetation zone in this region. Different ecological races occupy habitats as varied as arctic tundra, high altitude steppe, Saharan desert oases, temperate coastal forest, vegetable gardens and citrus orchards. However, the western United States and Canada is the only part of the range of the *P. machaon* group with extensive sympatry between species. All other regions support only a single species, or a contact zone between two species which is maintained in part by habitat segregation.

Studies of populations of the *P. machaon* group in sympatry are few, based principally on samples from geographically distant localities. Comparisons among many samples show either marked phenetic or ecological differences or a confusing interplay of character variation. Clearly, intensive surveys are needed of population variation in regions of sympatry or parapatry between major species of the *P. machaon* group. As well, there has been little explicit recognition of natural hybridization among species in the group. Since there is evidence of hybridization among the three species included in this study, and virtually all studies on hybrid zones in other taxa involve only two species, work on the *P. machaon* group is of significance to the general study of hybrid phenomena.

Historical Perspective

The historical context of work on the *machaon* group has influenced many of the resulting taxonomic decisions. In particular, the pattern of exploration of new regions and changing

motivations for research have left a diverse legacy of names for taxa. These names represent a number of major stages in the development of systematics as a separate discipline.

The recognized starting point for modern taxonomy, Linnaeus' *Systema Naturae*, Tenth Edition (1758), contained the description of *P. machaon* itself, the type species for the genus *Papilio* and, by extension to the Papilioniodea, it is the type species for all butterflies. New names such as *P. polyxenes* (Fabricius, 1775) and *P. asterius* (Stoll, 1782) were also published in that early period of endeavor to provide a full description of nature and what were perceived as God's works.

A steady stream of taxonomic descriptions followed, in step with the economic conquest of the remaining parts of North America and Eurasia. These provided a sense of the primacy of order, and the security and power of knowledge, for the growing class of people who engaged in this uniquely western activity. In addition, the practice of figuring the name of the author prominently behind the name of a taxon ensured that considerable effort and money was expended in the race to acquire this form of immortality. *Papilio zelicaon* was described by Lucas in 1852 under such circumstances, edging out Boisduval's (1852) *P. zolicaon* by a matter of a few months (Dos Passos, 1962). Obviously new species were exhausted relatively quickly, while the plethora of geographic races in the species of the *P. machaon* group provided an excuse for new names that has not been exhausted to this day. Subspecies names became fashionable around the turn of the last century and many of the older names were subsumed under the very oldest names. The most recent treatment of *Papilio machaon* throughout Eurasia (Seyer, 1974,1976a,1976b,1977) recognizes 36 subspecies in that region alone and synonymizes many more names.

The settlement of western North America in the latter part of the 1800's was integrally associated with many new names. *P. machaon aliaska* was contributed by Scudder (1869), based on material collected by an American lieutenant in a "Russo-American Telegraph Expedition" to Alaska. W.H. Edwards added a number of other names in the same sort of environment. He became wealthy through investments in the expanding railway industry of this period, and his financial security allowed him to play an important role in North American butterfly taxonomy. To the *Papilio machaon* group he contributed the names *P. bairdii* (1866), *P. oregonius* (1876) and *P. nitra* (1884), among others. Several of these taxa are treated in this study.

The discovery and classification of new taxa saw a watershed of sorts in the Victorian era. The abundance of newly collected specimens led to a new understanding of their inexhaustible variation and yet also to a philosophical rift among taxonomists. Darwin's publication of **The Origin of Species** (1859) provided a starting point for this process. By 1883 W.H. Edwards was arguing that criticism of his species designations in the *P. machaon* group was tantamount to a refusal of the teachings of Darwin, which was in turn equivalent to failing to admit the truths of Copernicus. Yet Edwards' names are an example of far greater emphasis on phenetic homogeneity and covariance than on hybridization information. This is particularly noticeable in his treatment of the *P. machaon* populations in the western United States, upon which he bestowed four specific epithets despite knowing that the forms the names referred to were probably all part of the same extended gene pool.

Hagen's (1882) report on the *P. machaon* group was published during the same period as Edwards' work, but showed the opposite tendency to that of Edwards. He looked for and found specimens with character states and combinations that were intermediate between those attributed to all the previously described forms. He concluded that all the North American

species of the *P. machaon* group (excluding *P. indra*) should be considered as local or climatic varieties of *P. machaon*.

Edwards' views prevailed among butterfly taxonomists, in part because David Bruce found that larvae of *P. bairdii* fed on *Artemisia dracunculus* Linneaus (Edwards, 1893 and 1895). This foodplant is a member of the Compositae, rather than the Umbelliferae or Rutaceae that are used by larvae of *P. zelicaon*. Also Bruce found that, in Colorado, *P. bairdii* adults were polymorphic for a yellow wing form which was much more like that of *P. oregonius* and *P. zelicaon* than the mostly black form it had previously been known for. However, Edwards' (1895) taxonomic response was to describe the yellow form from Colorado as yet another new species, *P. brucei*. This conflict between an increasing understanding of evolutionary phenomena such as polymorphism and the need for comprehensible, consistent classifications has continued to provide friction today.

Lord Walter Rothschild dealt with this conflict in a more balanced fashion. He was the epitome of acquisitiveness in the dying days of Victorian thought (Rothschild, 1983), and played a positive role in the systematics of the *P. machaon* group. His curator, Karl Jordan, contributed substantially to putting taxonomic practice in better accordance with evolutionary principles such as geographic differentiation (Mayr, 1955). Rothschild and Jordan consistently and accurately applied the concept of geographic races to their formal recognition of subspecies, and by this contributed to a lasting reduction in the number of taxonomic names used in the *P. machaon* group. Interestingly enough, they saw some specimens from west of Calgary from the same *P. machaon X zelicaon* hybrid populations which piqued my own interest in the group. They continued to use relatively traditional assignments, but remarked on the close resemblance of the black individuals from this area to the black forms of *P. bairdii* (Rothschild and Jordan, 1906).

The 1930's saw a fresh burst of new names proposed for taxa within the *P. machaon* group. Several of these were described from western Canada and Alaska. A. H. Clark (1932) contributed *P. machaon hudsonianus* from the boreal zone of northern Manitoba and Ontario, and *P. machaon petersi* from Alaska. Chermock and Chermock (1937) described *P. machaon* race *avinoffi* and *P. nitra* form *kahli*, both from the Riding Mountains of central Manitoba. McDunnough (1939) described *Papilio machaon dodi* from the prairies of southern Alberta and Saskatchewan. A number of new taxa were also described for the rest of North America during this period, while Eller (1936) produced a major monograph on the races of *Papilio machaon* in Eurasia. Eller (1939) followed this with a shorter treatment of the *P. machaon* group worldwide, in which he, like Hagen (1882), classified all North American taxa except *P. indra* as subspecies of *P. machaon*.

The names *P. machaon avinoffi* and *P. m. petersi* are now generally accepted as synonyms of *P. m. hudsonianus* and *P. m. aliaska*, respectively. *P. m. dodi* is accepted as a valid taxon, but is variously placed as a subspecies of *P. machaon*, *P. bairdii*, or *P. oregonius*. *P. nitra* form *kahli* was elevated without explanation to species status by Wilson (1961) and has generally continued to be used in that manner. Eller's work was rejected in North America, and cited as an example of poorly informed taxonomy (Remington, 1968a).

During the late 1950's, an understanding of the *Papilio machaon* group was placed on a rather different footing. The technique of mating *Papilio* by hand was described in detail by Clarke (1952), and Clarke collaborated in obtaining numerous hybrids in the following years, many of them within the *P. machaon* group (Clarke and Knudsen, 1953; Clarke and Sheppard, 1953, 1955a, 1955b, 1956a; Clarke *et al.*, 1977). Hand pairing became a commonly used

technique in hybridizing even distantly related species within the genus *Papilio*. The papers which Clarke co-authored with Sheppard have been the best studies to date on the genetics of the adult and larval color patterns of various taxa within the *P. machaon* group. They extended their experiments to other species of *Papilio* and produced a number of classic works, including studies on the African mimetic complex of *P. dardanus*. (The understanding of the interactions of genes which was gained from these hybridizing experiments was applied to the prevention of rhesus haemolytic disease in newborn humans, and Clarke was eventually knighted for his work.)

In the United States, Remington also conducted numerous hybridization and rearing experiments on the *P. machaon* group. His first report (1956) on this work was concerned with a collecting trip made to the Riding Mountains to obtain *P. nitra* form *kahli*, but he did not fully publish any of this research. His last report (1968a) included a description of a new species closely allied to *P. zelicaon*. The separation of Remington's *P. gothica* (1968a) was based on the hybrids it produced, as well as slight color pattern and ecological differences from *P. zelicaon*. Sibling species were in fashion in the evolutionary biology and systematics of the time, since they confirmed the primacy of genetic considerations in species definitions. However, Remington's *P. gothica* was soon criticized for a variety of reasons (Clarke and Sheppard, 1970; Shapiro, 1975; Emmel and Shields, 1980) and the only remnant of his concept survived in the form of a subspecific division of *P. zelicaon*.

The name of Remington's (1968a) taxon was later changed to *P. zelicaon nitra* on the basis of hybridization and rearing studies by Fisher (1977). These showed that Edwards' (1884) *P. nitra* was just a dark form of *P. zelicaon*, produced by a single dominant allele. Fisher theorized that the black form had arisen through the introgression of genes from *P. polyxenes*, like Remington's (1956, 1958) earlier thoughts on the origin of *P. nitra* form *kahli* through hybridization between *P. machaon* and *P. polyxenes*.

One of Remington's students, S. Ae, also carried out numerous hybridizations of *Papilio* species. He continued this work for more than two decades in Japan, publishing numerous progress reports and culminating in a major paper on *Papilio* phylogeny (Ae, 1979). He showed that even relatively distant interspecific crosses could produce adults, and many crosses between species within the *P. machaon* group had a reasonable degree of F1 viability. Ae's work is the tip of a veritable iceberg of *Papilio* hybridization studies, carried on by numerous enthusiasts, usually amateur, who rarely if ever publish. Similar situations can be found in saturniid and killifish circles, where the considerable effort to do such work seems to be maintained by a joy derived from the creation of new kinds.

During the last 15 years a substantial number of publications have appeared about the ecology of various members of the *P. machaon* group. These include studies of oviposition behavior (*e.g.,* Wiklund, 1981), larval growth (*e.g.,* Scriber and Feeny, 1979), diapause dynamics (*e.g.,* Sims, 1980) and pupal color determination (*e.g.,* Smith, 1978), among others. Although aimed at an ecological audience, they demonstrate a diversity of potential adaptive mechanisms. A consequence to systematic studies of the *P. machaon* group is that they show how numerous ecological races could have arisen, even within the last century (Shapiro and Masuda, 1980), as variations derived from a single basic gene pool.

There is considerable potential for future research on the *Papilio machaon* group. Clarke and Sheppard (1955b) stated that "It is clear that the Machaon-group provides some of the most suitable material ever investigated in animals for studying the process of speciation in detail, taking into account genetic, ecological and behaviour differences as well as time". I

agree wholeheartedly with this view, in part because the wide variation present within this group of beautiful butterflies makes genetic investigations relatively tractable.

However, study of the *P. machaon* group is also interesting because the variety of hybrid interactions poses conceptual problems in understanding the nature and origin of species. Such hybrid interactions "contrast two views of the species: as a set of populations delimited by genetic barriers to gene exchange; and as a set of populations maintained in a particular stable equilibrium by selection" (Barton and Hewitt, 1985). The appropriateness of study of the *P. machaon* group to an examination of species concepts is illustrated by the fact that Hagen (1882) and Edwards (1883) expressed similar opposing views a century ago.

MATERIALS AND METHODS

Acquisition of Specimens

I examined about 1200 specimens from my own collection, and about 2000 from the collections of the individuals and institutions listed in Table 1. The majority of material from my own collection, including the holotype and a series of paratypes of *P. machaon pikei*, have been deposited at the Canadian National Collection, Ottawa. Voucher specimens have been deposited at the University of Alberta Strickland Museum, as well as locality listings for all specimens examined in the course of this study.

I tried to obtain as many specimens as possible from each of a number of localities located in a rough grid pattern with intervals of 150–200 km across Alberta and northern British Columbia. I collected 20 or more adults from most of these localities, though I had to return to several of them a number of times in different years to do so. These localities comprise much of the geographic survey portion of my study, and are compared to more widely spaced localities in the remainder of western Canada and adjacent United States. I sampled most of the Alberta and northern British Columbia localities several times throughout the summer. Some population samples include adults obtained from larvae collected within about five km of a hilltop locality, as well as specimens from the hilltop itself. They have been distinguished from the wild-collected adults in the sections dealing with foodplant associations. Wherever possible, material taken by other collectors at or near a major locality was included in the morphometric portion of my study.

During the summers of 1980 through 1984 I collected about 650 adults of the *Papilio machaon* group, mostly on hilltops and prominent edges of river banks in Alberta and northern British Columbia. For some samples, I obtained pupae through the mail from other collectors. These included all the samples used in electrophoretic analysis for *P. polyxenes*, as well as most of the material from the *P. polyxenes X machaon* hybrid zone and most of the *P. zelicaon* specimens from southern British Columbia. I also collected about 1800 larvae during 1980–1984, and reared about 450 of these to the adult stage on the same foodplant from which the larvae has been collected. All larval records are listed in Table 14.

Pressed samples of all new foodplant records were identified by Dr. J. G. Packer, Department of Botany, University of Alberta. Records attributed to individuals other than me were identified by those individuals.

Table 1. Sources of specimens examined of the *P. machaon* species group

Names of Curators of institutional collections are listed at ends of entries.

Acorn, J.H., Dept. of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada

Alberta Provincial Museum, Natural History Dept., 12845-102 Ave., Edmonton, Alberta, T5N OM6 Canada (A.T. Finnamore)

Allyn Museum of Entomology, Sarasota, Florida, 326111 U.S.A. (L.D. Miller)

Bird, C.D., Box 165, Mirror, Alberta, T0B 3C0 Canada

British Columbia Provincial Museum, Parliament Buildings, Victoria, British Columbia, V8V 1X4 Canada (R.A. Cannings)

British Museum (Natural History), Cromwell Road, London, SW7 5BD, England (R.I. Vane-Wright)

Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6 Canada (J.D. Lafontaine)

Guppy, C.S., 4120 St. Georges Ave., North Vancouver, British Columbia, V7N 1W8 Canada

Hilchie, G.J., Dept. of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada

Hooper, D.F., Somme, Saskatchewan, S0E 1N0 Canada

Hooper, R.R., Box 205, Fort Qu'Appelle, Saskatchewan, S0G 1S0 Canada

Klassen, P., Box 212, Elm Creek, Manitoba, R0G 0N0 Canada

Kohler, S.J., Forest Insect and Disease Section, Montana Department of Natural Resources and Conservation, 2275 Spurgin Road, Missoula, Montana, 59809 U.S.A.

Kondla, N.G., 22 Brock Place, Lethbridge, Alberta, T1K 4C7 Canada

Krivda, W., 319 Crossley Ave., The Pas, Manitoba, R9A 1B7 Canada

Pike, E.M., 1410-4th Ave. N.W., Drummheller, Alberta, T0H 1L0 Canada

Royal Ontario Museum, Dept. of Entomology, 100 Queens Park, Toronto, Ontario, M5S 2C6 Canada (R. Jaagumagi)

Saskatchewan Museum of Natural History, Wascana Park, Regina, Saskatchewan, S4P 3V7 Canada (R.R. Hooper)

Shepard, J.H., Sproule Creek Road, RR#2, Nelson, British Columbia, V1L 5P5 Canada

Shigematsu, S., 2314-22nd St. S., Lethbridge, Alberta, T1K 2K2 Canada

Sperling, F.A.H., Box 31, Bragg Creek, Alberta, TOL OKO Canada

University of Alberta, Entomology Dept., Strickland Museum, Edmonton, Alberta, T6G 2E3 Canada (G.E. Ball & D. Shpeley)

University of British Columbia, Zoology Dept., Spencer Entomological Museum, Vancouver, British Columbia, V6T 2A9 Canada (S. Cannings)

University of Calgary, Biology Dept., Calgary, T2N 1N4 Canada (G. Pritchard)

University of Manitoba, Entomology Dept., Winnipeg, Manitoba R3T 2N2 Canada (R.E. Roughley)

Waterton National Park, Interpretation Administration, Waterton, Alberta, T0K 2M0 Canada

Table 2. Descriptions of morphometric characters of adults and larvae of the *P. machaon*
group, used in multivariate analyses

Numbering of character states is the same as that used in multivariate analyses.

A. Extent of yellow scaling in cell Cu2, in anal margin of dorsal hindwing (Fig. 2)
    1.   All except a few yellow scales are restricted to area from inner margin of median dark band to less than halfway to divergence of veins Cu2 and Cu1. (*e.g.*, Fig. 3)
    2.   Virtually all yellow scales restricted to area between median band and divergence of Cu1 and Cu2.
    3.   Yellow scales extend past junction of Cu1 and Cu2, but less than halfway between Cu1-Cu2 junction and wing base.
    4.   Yellow scales extend from median band to more than 3/4 of way to wing base. (*e.g.*, Fig. 2)
B. Shape of pupil in anal eyespot of dorsal hindwing. (Fig. 1)
    1.   Thin line at lower edge of blue region, connected to wing margin. (*e.g.*, Fig. 1a)
    2.   Club shaped, in that thinnest portion near margin is less than half the width of thickest portion closer to center of eyespot. (*e.g.*, Fig. 1b, 2, 3)
    3.   Oblong spot at lower edge of red area, not connected to margin. (*e.g.*, Fig. 1c)
    4.   Round spot centerd in red area, generally with less than two times as much red above pupil as below it. (Fig. 1d)
C. Extent of black scales between blue and red portions of anal eyespot of dorsal forewing.
  (Fig. 1-3)
    1.   Black line extending along less than 1/4 of blue-red boundary. (*e.g.*, Fig. 1a)
    2.   Black line separating blue from red along between 1/4 and 3/4 of the width of anal eye. (eg. Fig. 1c)
    3.   Black line separating more than 3/4 of blue from red (boundary line may be wide or narrow).(*e.g.*, Fig. 1b,1d,2,3)
D. Color of hairs on tegula. (Fig. 4 and 6)
    1.   Virtually all hairs on tegula yellow. (*e.g.*, Fig. 4a-b and 6a-e)
    2.   Less than half as much yellow on tegula as in typical yellow morph adults but more than about 15%. (*e.g.*, Fig. 4c)
    3.   Virtually all tegula hairs black. (*e.g.*, Fig. 4d)
E. Extent of yellow scales in basal half of disc of central forewing. (Fig. 5)
    1.   Yellow scales in more than 50% of area. (*e.g.*, Fig. 5a)
    2.   Thick streaks or a more general flush to less than 50% of total area. (*e.g.*, Fig. 5b)
    3.   Few thin streaks or a light sprinkling of yellow scales. (*e.g.*, Fig. 5c)
    4.   Virtually no yellow scales in basal half of disc of ventral forewing. (*e.g.*, Fig. 5d-e)
F. Extent of yellow scales of postmedian yellow band in apical cell of ventral forewing.
  (Fig. 5)
    1.   Postmedian spot large, occupying more area than bordering black scales. (*e.g.*, Fig. 5a-c)
    2.   Definite patch of diffuse yellow, but occupying less area than black scales. (*e.g.*, Fig. 5d)
    3.   Virtually no postmedian yellow scales in cell. (*e.g.*, Fig. 5e)

Table 2 (continued)

G. Number of cells with orange patch in postmedian area of ventral hind wing. (Fig. 3)
    1.   No cells with a distinct patch of orange cells on distal side of postmedian yellow area.
    2-8. The total number of cells, plus one, which have a distinct patch of orange, up to a total of 7 cells. Postmedian wing cells which are covered in only black scales are assumed to have an orange patch, as in some female *P. polyxenes*.

H. Amount of yellow hair on metathorax below base of hindwings. (Fig. 6)
    1.   Yellow hairs extend around the ventral part of metathorax. (*e.g.,* Fig. 6a)
    2.   Substantial patches of yellow hairs on each side of metathorax which do not meet ventrally. (*e.g.,* Fig. 6b-d)
    3.   All metathoracic hairs black, or at most a very few short yellow hairs restricted to immediate base of wing. (*e.g.,* Fig. 6e-f)

I. Ventral abdominal line. (Fig. 6)
    1.   All abdominal segments with distinct ventral line of yellow hairs along sagittal plane. (*e.g.,* Fig. 6a)
    2-9. The total number of segments, plus one, which do not have a distinct patch of yellow scales or hairs along sagittal line. Start counting from first abdominal segment after thorax, to a maximum of 8.

J. Lateral abdominal yellow. (Fig. 6)
    1.   Broad band of yellow on each side, extending along length of abdomen (male claspers excluded). (*e.g.,* Fig. 6a-d)
    2.   Large square lateral spots on some or all abdominal segments, with narrow divisions between spots. (*e.g.,* Fig. 6e)
    3.   Small round lateral yellow spots on all or most segments, distance separating spots generally greater than width of spots. (*e.g.,* Fig. 6f)

K. Upper abdominal spots. (Fig. 6)
    1.   All abdominal segments with a distinct pair of subdorsal yellow spots, separated from lateral abdominal band or line of spots (character J., above). (*e.g.,* Fig. 6e-f)
    2-9. The total number of segments, plus one, which do not have at least one yellow spot distinct from yellow line.
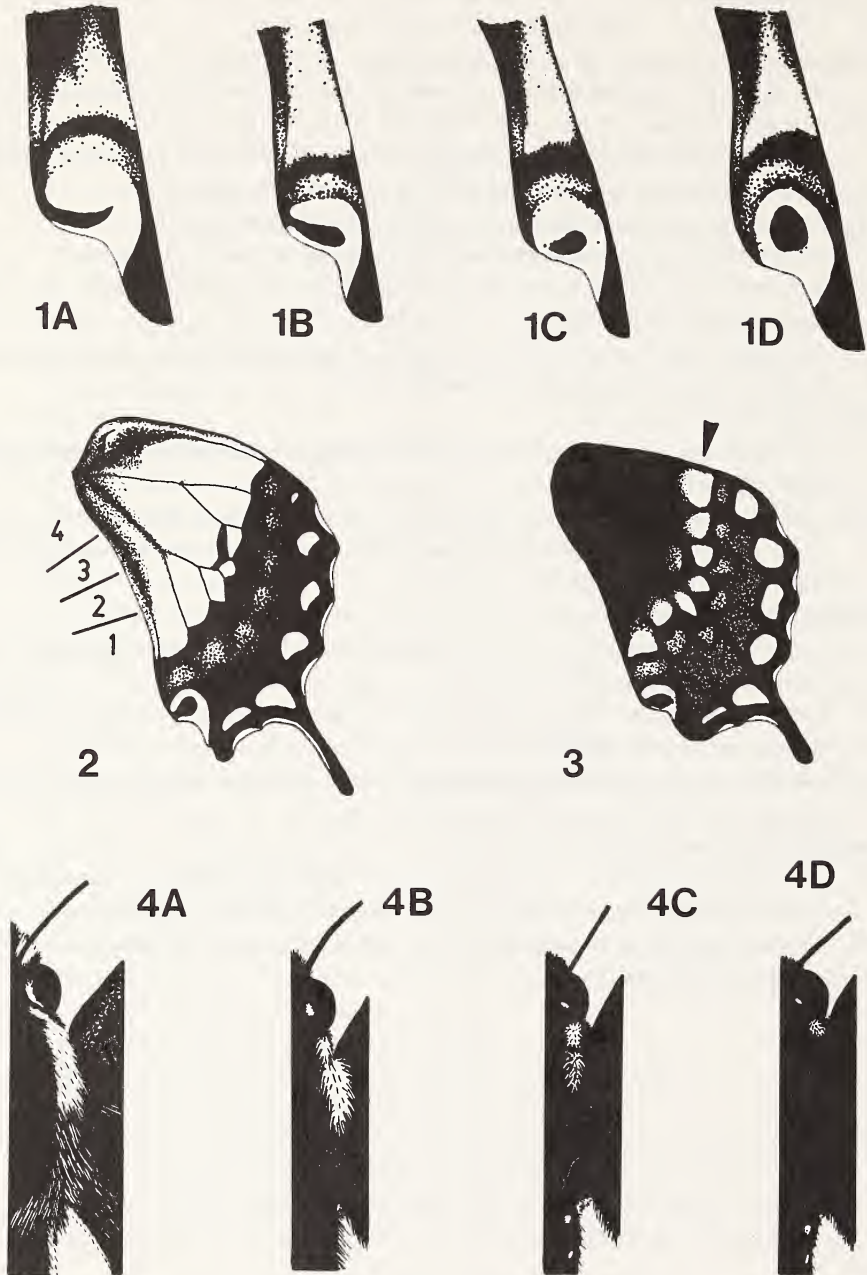
Figures 1 to 4. Figure 1. Anal eyespot of dorsal hind wing: A, *P. m. aliaska* Mi. 391, Alaska Hwy., British Columbia. B, *P. m. dodi* Nacmine, Alberta. C, *P. zelicaon X machaon* Nacmine, Alberta. D, *P. zelicaon* Wintering Hills, Alberta. Figure 2. Yellow scaling of dorsal hindwing anal margin *P. m. oregonius*, Brewster, WA. Character states for yellow anal scales are numbered beside figure. Figure 3. Ventral hindwing, with location of orange scales *P. p. asterius*, Karlsruhe, North Dakota. Arrow shows postmedian band, which contains orange scales. Figure 4. Dorsal view of thorax, showing tegula: A, *P. zelicaon* yellow morph Wintering Hills, Alberta; B, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; C, *P. p. asterius* Karlsruhe, North Dakota; D, *P. p. asterius* Karlsruhe, North Dakota.
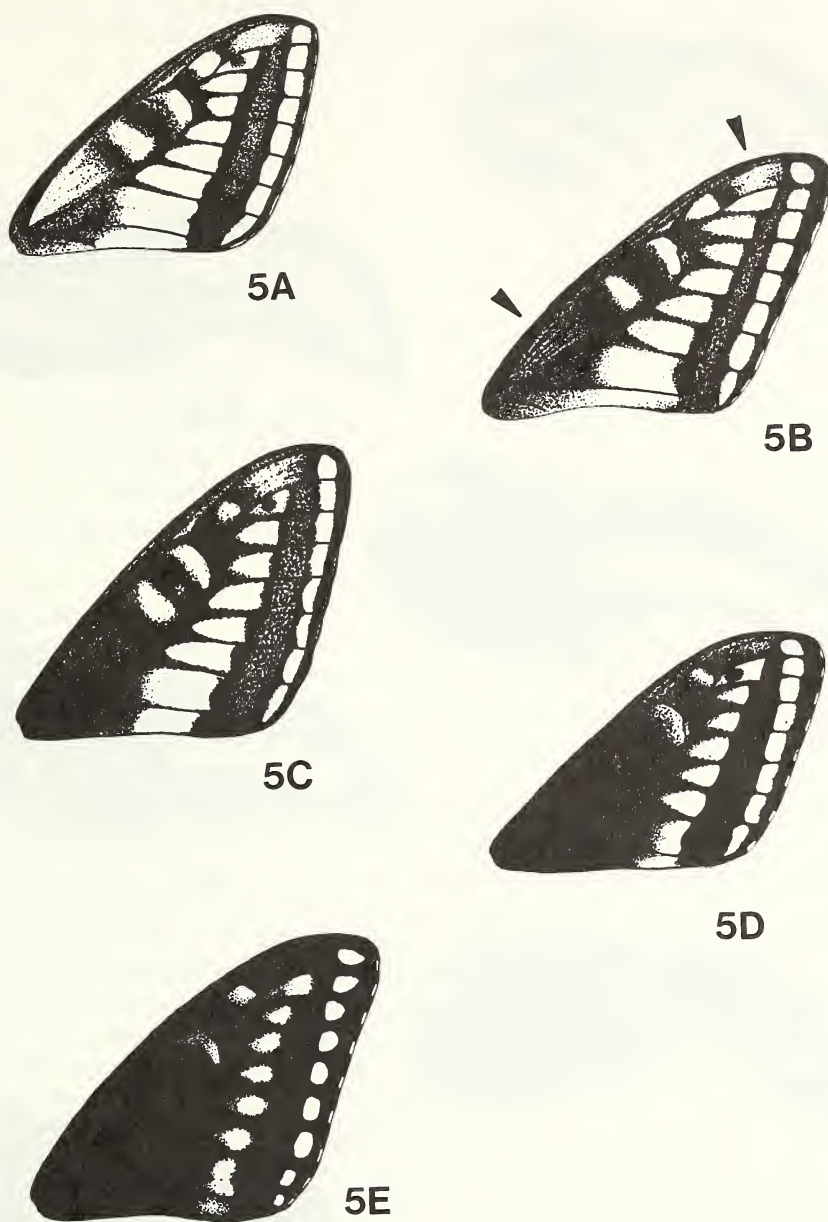
Figure 5. Yellow scales on disc and apex of ventral forewing. Arrows on Figure 5b show location of disc and apical cell: A, *P. m. aliaska* Pink Mountain, British Columbia; B, *P. m. dodi* yellow morph Nacmine, Alberta; C, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; D, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; E. *P. p. asterius* Karlsruhe, North Dakota.
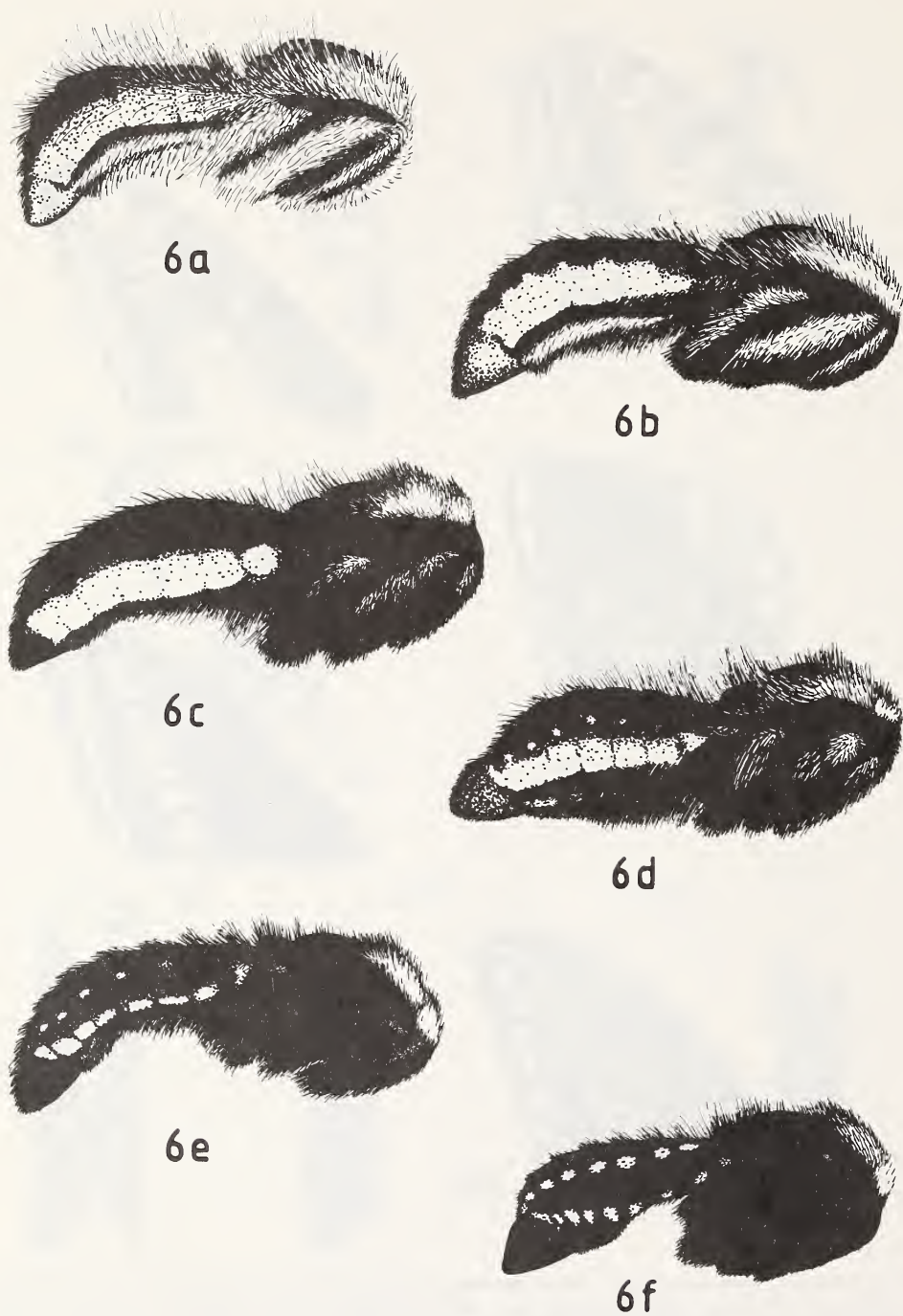
Figure 6. Lateral view of thorax + abdomen. Wings and head have been removed. a, *P. m. aliaska* Pink Mountain, British Columbia; b, *P. m. dodi* yellow morph Nacmine, Alberta; c, *P. zelicaon* yellow morph Wintering Hills, Alberta; d, *P. zelicaon X machaon* yellow morph Bragg Creek, Alberta; e, *P. zelicaon X machaon* black morph Bragg Creek, Alberta; f, *P. p. asterius* Karlsruhe, North Dakota.

Table 3. Names, sources and quantities of proteins, and conditions of gels used in electrophoretic analyses of specimens of the *P. machaon* species group.

Protein		Gel		Homogenate (microliters)	
Symbol	Name	%	pH	Thorax	Abd.
αGPD	α-glycerophosphate DH	9.0	8.9	5	5
G-6-PD	glucose-6-phosphate DH	6.0	8.9	25–30	5–10
IDH	isocitrate DH (NADP)	9.0	8.9	30	15–20
MDH	malate DH	9.0	8.9	5	5
ME	malic enzyme	4.5	8.2	15	30
ODH	octanol DH	9.0	8.9	50	30–50
APK	arginine phosphokinase	7.0	8.9	25	–
Est4 & 5	esterases	7.0	8.9	30	–
Prot1 & 2	general protein	7.0	8.9	20–25	–

Characters Examined

Morphometric characters.— Eleven morphometric characters, defined in Table 2, and illustrated in Figures 1 to 6, were scored for adults used in this study. Individuals were scored against both the written descriptions of character states and a number of standard specimens. Standard and illustrated specimens were labelled as such and are in the Strickland Museum, University of Alberta.

The choice of characters for analysis was made for the following reasons:

1. The characters had been used previously by other workers for distinguishing between species. Those listed by Remington (1968a), were especially useful in this regard, because of the clear manner in which they were defined. This allowed me to relate populations in western Canada to particular species concepts developed elsewhere in North America, and also to test diagnostic structural characters against variation in electrophoretic characters.

2. The characters had to be fast and easy to score by eye, and hence allow accurate processing of numbers of specimens in a relatively short time.

3. There had to be a large amount of variation in character states expressed in the major study area, western Canada. The purpose of this criterion was to maximize the likelihood that useful information would be recorded when a character was scored.

4. Characters were chosen which appeared to vary fairly independently of each other within populations, to maximize the likelihood of sampling the effects of several different genes, and hence of obtaining information of significance to gene flow between populations. I tried to minimize the number of times I scored the presence of the gene for black color, which is known to affect a large area of the adult wings and body (Clarke and Sheppard, 1953, 1955b and 1956a; Fisher, 1977).

I also recorded color of spots on each larva. Spot color was determined by eye and by comparing larvae against each other. I did not use consistently a standard for comparison, but I judge error in assignment of larvae to either a yellow or an orange group to be small. Orange spotted larvae included both the pale orange and bright orange groups delineated by Clarke and Sheppard (1955b). Records were also obtained by contacting lepidopterists who had reared

larvae in western Canada, and by examining published records for spot color for the whole *P. machaon* group.

Electrophoretic characters.— A total of 860 adults of the *Papilio machaon* group were used in electrophoretic analyses. These were frozen live and maintained at -20 C, and most were homogenized within a few weeks of being frozen. However, bands were still readable for whole specimens kept frozen for more than two years.

Tissue for electrophoresis was obtained by dissecting thoracic and abdominal contents from specimens which had been allowed to thaw on ice just before use. The corpus bursa of females was not used, since it may have contained male spermatophores. After tissue had been removed, specimens were pinned through one side of the thorax and mounted in the manner standard for Lepidoptera curation. Each specimen was given a unique number and labelled to allow the morphometric and electrophoretic character states to be correctly associated.

Thoracic and abdominal tissue samples were homogenized separately, each in 0.2 ml homogenizing solution. Homogenate not used immediately was frozen and stored at -20 C in the centrifuge tubes. Most samples gave interpretable bands from frozen homogenate, though esterases and IDH deteriorated the most rapidly when subjected to successive freeze-thaw cycles.

The electrophoretic apparatus used was the same as that described by Rolseth and Gooding (1978), in whose laboratory and under whose direction I did the preliminary work for this study. Some changes have been made in their methods since publication. These include: 1) making the "B" solution with 25.6 ml of 1M H_3PO_4, 5.7 gm Tris and 0.46 ml TEMED, brought up to 100 ml with distilled water; 2) making the homogenizing buffer with 7.0 ml H_2O, 1.0 ml B, .300 gm polyvinylpyrolidine and 40 mg DL-dithiothreitol; 3) forming stacking gels with 20 slots; and 4) sealing the edges of the apparatus with parafilm rather than a plug gel. Also gels were used at pH 8.9 and pH 8.2, using 24 ml and 60 ml of 1M HCl, respectively, in the stock "A" solution. Tissue was electrophoresed at 40 milliamp/gel for 2.0 hours in pH 8.9 gels, and 3.5 hours in pH 8.2 gels. Electrophoresis conditions for the loci used in this study are noted in Table 3; Rf values listed in Tables 6 and 13 refer to electrophoresis performed under these conditions.

Except for the use of $MgCl_2$ rather than $MnCl_2$ as a cofactor for IDH, staining methods are fairly standard applications of recipes available in Shaw and Prasad (1970) or Brewer (1970). Both esterase loci showed much greater activity with α-naphthyl acetate than with β-naphthyl acetate or AS-D-acetate, and were not significantly inhibited by eserine. APK was usually stained with Coomassie blue, since it seemed to be the most common protein that could be resolved by this method in thoraces. The identity of the APK bands was ascertained in several homozygous individuals and the single individual (a male) with an allelic variant, using the staining technique of Gooding and Rolseth (1979).

I stained for a variety of other enzymes, using recipes of Brewer (1970), Shaw and Prasad (1970) and Menken (1980). These included ADH (with ethanol, isopropanol and sorbitol), AO (with benzaldehyde and heptaldehyde), GLUO, GDH, GA-3-PD, GlyDH, LDH, G6PDH, SDH, TO and XDH. In these attempts, bands were either very faint or did not appear.

All except three of the protein loci stained were dimers, while APK and Est4 were monomers, and ME may have been a tetramer. None of the loci included in this study, except possibly APK, were sex linked. Heterozygotes were present in both sexes for all other loci, including G-6-PD, which is frequently sex linked in other taxa.

The genetic inheritance of alleles was not checked through breeding experiments. However, since most of the local populations surveyed had allelic distributions that were at Hardy-Weinberg equilibrium proportions, environmental induction of particular alleles seems unlikely. Also the general distribution of alleles showed an excellent correspondence with morphometric, and ultimately taxonomic, characters.

In any event, my taxonomic conclusions are not strictly dependent on genetic interpretations of protein banding patterns. The bands are treated as equivalent to any other taxonomic character and are more discrete than the character states in my morphometric analysis. An additional advantage of the electrophoretic characters I used is that they probably represent a relatively unbiased selection of loci. The choice of loci for staining was influenced by my ability to obtain bands consistently and my ability to interpret variation in a consistent manner, both of which factors are independent of the morphometric characters measured.

Numerical Analyses

Principal components analysis (PCA) helps to visualize clusters in multivariate data, is relatively assumption-free, and provides a basis for internally consistent, simple comparisons of both individuals and populations. PCA seems to give fairly accurate representation of distances between data points, and has been used successfully in studies of hybrid swarms (Neff and Smith, 1979; Pimentel, 1981). Relatively few characters appear to be required to elucidate patterns of racial variation. Thorpe (1985) showed that patterns with 90% confidence could be obtained from as few as 8–10 characters in grass snakes in Europe. Also, it is easy to relate samples not used in the initial analysis to those that were, by applying factor loadings.

Three major PCAs were applied to an initial group of 728 specimens, almost all of which were from western Canada and particularly Alberta, and all I had available, in early 1984, with complete scores for all morphometric and electrophoretic characters considered in this study. An effort had been made prior to this to obtain a reasonably broad sampling of the different geographic populations and morphotypes known from the region, including those described by other authors. One PCA was performed on only the morphometric characters, one on only the electrophoretic characters and one on the combined morphometric and electrophoretic characters together. The same individuals were used in all three PCAs, to give a more meaningful basis for comparison of variation in character patterns. Then the factor loadings were applied to individuals which could only be completely scored for one of the two main character suites.

Discriminant function analysis (DFA) was applied to subgroups where PCAs did not give clear indications of the number of species in a region or the nature of distinctions among them. DFA was applied to reared adults obtained from southern and south-central Alberta, where adults from different major populations showed only slight separation into the major groups distinguished in other regions. Discriminations were based on the different foodplants, on which larvae were collected. DFA was also applied to the geographically separated subspecies of *P. machaon*, to give an assessment of the accuracy of identification of specimens.

All work for this section of the study was carried out with the Midas statistical package (Fox and Guries, 1976) on the Amdahl computer system at the University of Alberta. The principal component function was used only with the "unscaled" option in this package. The 11 morphometric characters were scaled before PCA or DFA, to make their ranges of variation equivalent. Scaling factors and PCA/DFA loadings are included in Tables 12 and 13. Electrophoretic character scores were not scaled, since these were already recorded in a manner

that gave equivalent weights to each character.

Electrophoretic characters were scored one allele at a time, for each butterfly. Each allele known from my work on the *P. machaon* group was considered a character with three character states and scored: 1), if the allele was absent; 2), if it was present with another allele at that locus; and 3), if it was present in the homozygous state. Of the 42 electrophoretic characters, only a small proportion were significant to the scores on the first few principal component axes. The APK locus was not used in PCA, because there was only one variant in 728 individuals.

An alternative method for scoring electrophoretic characters is used in some numerical analyses (Mickevich and Mitter, 1981; Buth, 1984), with each locus a character, and each allele coded on the basis of its relative mobility. This method was rejected because it does not allow distinction between an individual homozygous for a particular allele, and an individual heterozygous for two alleles located an equal distance on either side of the homozygous allele. This situation occurred frequently at the G-6-PD locus.

Electrophoretic data were also analysed using the Biosys-1 package of Swofford and Selander (1981). Allele frequencies, heterozygosity indices and tests for Hardy-Weinberg proportions were calculated. All individuals with partial electrophoretic information were used, giving a total sample size of 860.

Hardy-Weinberg equilibrium measures provided tests of gene pool homogeneity, and complemented the multivariate clustering techniques. First, the entire sample for a region was tested as a whole before being divided into major groups which might be different species. If the subsets were much closer to equilibrium after the subdivision, this was considered evidence of a significant degree of gene flow within but not between the subgroups. Excess homozygosity may be due to other factors as well, such as the presence of null alleles or temporal and spatial variation within samples. I consider these possibilities unlikely in the context of this study, since the occurrence of excess homozygosity coincided fairly well with taxonomic expectation.

Taxonomic Interpretation and Conventions

I view species concepts as a balance between practicality and meaningfulness. Strict definitions can be established, but they may not distinguish populations of biological relevance. Alternatively, if a species concept is particularly vague or difficult to apply in practical situations, then its potential biological meaningfulness is of little use. Both practicality and meaningfulness should be assessed in terms of the reason for naming species, which is the identification of organisms in a way that allows the user of the name to efficiently communicate information about their relationships with other organisms.

Some taxonomists, for example Blackwelder (1967), view species recognition as a sort of learned trade which cannot be precisely characterized or defined. Here species are kinds of primary concepts. Understanding how to interpret certain kinds of information becomes a matter of developing a sense of similarity relations and applying it in a manner sanctioned by experienced peers. This part of taxonomic training thus involves the transfer among individuals of a conceptual paradigm, in the sense of Kuhn (1970).

However, the uses of systematics are primarily scientific, and there is a need to make its operations repeatable, quantifiable and testable. Most systematists have acknowledged that species tend to be clusters of like individuals, and many of them have focussed on this aspect. Even workers whose main research objectives are in elucidation of evolutionary mechanisms may begin their discussion of species by referring to them as "discontinuous arrays" (Dobzhansky *et al.*, 1977:166). However, some systematists treat species as phenetic covariance

clusters, and de-emphasize reference to reasons for the existence of these clusters. Examples include Ehrlich (1961), who identifies species as relatively arbitrary groups of organisms delineated by overall character similarity, or Neff and Platnick (1981:12), who characterize species as "the smallest detected samples of self-perpetuating organisms that have unique sets of characters". This view appears strongly influenced by the desire to make the process of distinguishing species as tractable as possible, particularly in terms of mechanical simplicity.

Other taxonomists emphasize the process perceived to maintain distinctions between species and unity within species, perceiving gene exchange as the characteristic that makes such a group of organisms a biologically coherent entity. A widely accepted definition of this type is that of Mayr (1969), who defines species as "groups of interbreeding natural organisms that are reproductively isolated from other such groups". However, species descriptions based on hybrid sterility are in some ways as arbitrary as species descriptions based on phenetic clustering, since the degree of hybrid fertility which is accepted before a specific distinction is recognized is itself an arbitrary procedure. One way of dealing with the latter objection has been to characterize different populations as species only if they exhibit 100% hybrid sterility (*e.g.,* Key, 1982). Unfortunately, this definition is so broad that many phenetically distinctive groups of organisms presently recognized as belonging to different species would have to be combined if the definition were rigorously applied.

The attempt to make the process of species recognition more objective thus seems to have led in two major directions: 1), grouping by phenetic covariance; or 2), by interbreeding data. However, grouping on the basis of either data type alone can lead to the absurd extreme of operationalism, in which a definition is conceived as no more than a corresponding set of operations (Hull, 1968). The main fault of operationalism is that it emphasizes practicality in the application of a definition, but restricts the flexibility and general usefulness of the definition.

The history of classification of the *P. machaon* group provides examples of both kinds of operationalism. W.H. Edwards' names are an example of an overemphasis on morphotypes, relative to hybridization information. On the other hand, Hagen's (1882) taxonomic conclusions show an overly strict adherence to the interbreeding criterion of his species concept; thus, he fell into the same trap of operationalism that reduced the value of Edwards' work.

Considering the ecological and genetic complexity of the *Papilio machaon* group, one should not expect sytematic research to have simple taxonomic consequences. I use numerical methods in a predominantly descriptive manner, to characterize the pattern of phenetic variation within and between populations. As in most taxonomic work, there is a need to distinguish variation at the level of local populations, geographic races and species. Geographic patterns of variation were first examined within major character suites, such as structural and electrophoretic characters, and then compared among suites. Finally, these patterns of variation were loosely interpreted in terms of current species concepts, especially through inferences of gene flow and the maintenance of identity in time and space.

Recognition of subspecies is somewhat more arbitrary. My main criterion for formally recognizing a differentiated series of populations or an ecological race as a subspecies is that 75% or more of the specimens can be distinguished without the aid of locality labels (*cf.,* Mayr, 1969). The main reason for using subspecies names is to relate my own findings to previous work, much of which has been couched in terms of description of new specific and subspecific taxa.

Since subspecies are preeminently geographic divisions of species, the former should be at least parapatric, with intermediates occurring along only a relatively narrow zone. Phenetic homogeneity within a subspecies should be quite high compared to that within zones of intergradation. Although most subspecies have been described on the basis of structural characters, ecological characters are also important indicators of substantial genetic distinctions.

The main difficulty in classifying populations and individuals of the *P. machaon* group from western Canada is that in some regions groups of individuals seem like genetically distinct entities in sympatry, while in other areas extensive hybridization occurs. In general, this difficulty is dealt with by continuing to recognize populations as separate species only if areas of sympatry without hybridization are much more extensive than areas in which substantial hybridization occurs. Examples in the *P. machaon* group are discussed in detail in the section on diagnosis of adults and ranking of taxa.

Populations composed predominantly of hybrid individuals were given names which reflect such hybrid origins. Since the International Code of Zoological Nomenclature (1985) does not provide rules for hybrid names, I follow the International Code of Botanical Nomenclature (1983), and more general guides in taxonomy such as Schenk and McMasters (1956). However, the convention of ordering parental names by the sexes which contributed to the hybrid swarms is not useful for the *P. machaon* group. Instead, the species epithets of the parental species are listed, with an "X" between them, so the first epithet indicates the species most similar to the majority of hybrid specimens.

I use form names as little as possible, because they have suffered from considerable unevenness of usage (*e.g.,* Scott, 1981) and have a limited communication value. A better alternative would be to concentrate on distinguishing genes and alleles, as Clarke and Sheppard did in the 1950's with polymorphisms in the *P. machaon* group.

CLASSIFICATION AND RECOGNITION OF TAXA

The taxonomic conclusions of the present study are presented before the supporting data, because I propose several changes to the systems of names which have been applied previously to the *Papilio machaon* group. To simplify presentation of data in succeeding sections, my system is summarized in the present section. Detailed reviews of characteristics of the included taxa follow, and are discussed in succeeding sections, which deal with evolutionary hypotheses.

Summary of Taxonomic Assignments

The following list is based on Miller and Brown (1981), and summarizes the disposition of all scientific names applying to the *P. machaon* group in western Canada and Alaska. It includes type localities, as well as names applying to populations which are found, or have at some time been considered to have been found, in the study area.

P. machaon Linnaeus, 1758:462. Type locality(TL)-Sweden.
a. *P. m. aliaska* S.H. Scudder, 1869:407. TL-Nulato, Alaska.
    =*joannisi* R. Verity, 1907:pl.10, Fig. 17. TL-Nulato, Alaska.
    =*petersii* A.H. Clark, 1932:8–9. TL-Kuyukok River, Alaska.
b. *P. m. bairdii* W.H. Edwards, 1866:200. TL-"Arizona", restricted to Fort Whipple,
    Arizona, by Brown (1975).

=*brucei* W.H. Edwards, 1895:239. TL-"Colorado", restricted to Glenwood
  Springs, Colorado, by Brown (1975).
c. *P. m. oregonius* W.H. Edwards, 1876:208. TL-near The Dalles, Oregon
  (neotype locality is at Hepner, Oregon [Brown, 1975]).
d. *P. m. hudsonianus* A.H. Clark, 1932:6–7. TL-Kettle Rapids, Manitoba.
e. *P. m. dodi* J. McDunnough, 1939:216–217. TL-Red Deer River, 50 miles N. E. of
  Gleichen, Alberta (probably near Dorothy [Kondla, 1981]).
f. *P. m. pikei* F.A.H. Sperling. NEW SUBSPECIES. TL-Dunvegan, Alberta.
P. zelicaon Lucas, 1852:136. TL-"California".
  =*nitra* W.H. Edwards, 1883:162–163. TL-Judith Mts., Montana.
  =*gothica* C.L. Remington, 1968:2–5. TL-Gothic, Colorado.
  =ab. *mcdunnoughi* J.D. Gunder, 1928:162. TL-Waterton Lakes, Alberta.
P. zelicaon X machaon NEW HYBRID MORPH
P. polyxenes Fabricius, 1775:444. TL-"America", restricted to Cuba by
  Rothschild and Jordan (1906).
a. *P. p. asterius* Stoll, 1782:194. TL-New York, Virginia and Carolina.
P. machaon X polyxenes NEW HYBRID MORPH
  =*avinoffi* F.H. and R.L. Chermock, 1937:11–12. TL-Whirlpool River,
  Riding Mts., Manitoba.
P. polyxenes X machaon NEW HYBRID MORPH
  =*kahli* F.H. and R.L. Chermock, 1937:12-13. TL-Riding Mts., Manitoba.

Papilio machaon pikei, new subspecies

Of the five major sections of *P. machaon* which occur in western Canada, four were described many years ago. The fifth occurs exclusively within the Peace River region, and appears to have been collected once (Llewllyn Jones, 1951) before being rediscovered by E.M. Pike and me in 1980. The Peace River race of *P. machaon* is ecologically distinct from *P. m. aliaska* and *P. m. hudsonianus*, and is geographically disjunct from *P. m. dodi* and *P. m. oregonius*. Although very similar in morphometric and electrophoretic features to the other subspecies of *P. machaon* in western Canada, it is as different from each of these as they are from each other. In order to facilitate discussion about the evolution of this race, it is described below. All measurements are based on specimens used in the principal components analyses in the following section.

Description.— *Adult* (Plate 1, e-f). *Male* (Plate 1, e). Mean forewing length, from base at thorax to apex, 40.8 mm (range 36.5–47.0). Dorsal hindwing with yellow scales extended over proximal portion of wing almost to base, except in cell Cu2, latter with yellow scales confined to postmedian region. Black pupil of dorsal hindwing eyespot along lower edge of red scales and connected to margin of wing. Pupil club-shaped or narrow line. Blue and red scales of eyespot separated by few or no black scales. Basal half of ventral forewing disc covered by yellow scales. Postmedian area of ventral hindwing of most specimens with distinct patch of orange scales in two or fewer cells. Thorax covered by long yellow hairs ventral to wings. Ventral side of abdomen with yellow hairs on all segments. Broad yellow lateral band on abdomen, extended over claspers. Subdorsal spots above lateral abdominal band in few specimens. *Female* (Plate 1, f). Like male, but larger (mean forewing length = 42.6 mm, range = 39.5–45.5), and with more rounded forewing.

Immatures. Eggs, larvae and pupae very similar in all stages to those of *P. m. oregonius* (see Perkins, *et al.*, 1968 for photographs) and to *P. m. dodi*. Fifth instar larvae with segmental spots orange or yellow, but most individuals with orange spots. Background color of mature larvae from flat blue-green to bright emerald green. Pupae either mottled brown or green, but not mixture of brown and green as in some specimens of *P. m. aliaska*. Larval foodplant *Artemisia dracunculus*, on warm, dry, eroding exposures.

Type series. Abbreviations: **f** = female, **m** = male, *Ad* = *Artemisia dracunculus*, E4# = F.A.H. Sperling electrophoresis number, CNC = Canadian National Collection. All reared specimens have pupal shell and some have fifth

instar larval skin attached to card below specimen. Pupation and emergence dates are omitted in the following list. Seventy eight paratypes have been deposited in public institutions, and 20 remain in the personal collection of E.M. Pike. Sites of deposition are listed in brackets behind each entry.

Holotype: male. Canada, Alberta; Dunvegan (s. Fairview); June 14, 1981; F.A.H. Sperling; [on dry, grassy, south-facing slopes above Peace River] (CNC).

Allotype: female. Canada, Alberta; Dunvegan; June 22, 1982; F.A.H. Sperling; e4# 546 (CNC).

Paratypes. 2f, 6m: Canada, B.C.; Attachie; larva coll. Aug 9 '81; F. Sperling; on *Ad*; e4# 521–526,528,529 [all emg. 1983], (CNC). 2f, 1m: Attachie, British Columbia; 35 km W. Ft. St. John; larva coll. Aug. 9, 1981; on *Ad*; [all emg. 1982]; F. Sperling (CNC). 1m: Attachie, British Columbia; 35 km W. Ft. St. John; larva coll. July 9, 1981; on *Ad*; F. Sperling (CNC). 1m: Taylor, B.C.; July 3 '80; F. Sperling (CNC). 1f: larva on *Ad* at Taylor, B.C. on Aug. 18, 1980; [emg. 1981]; F.A.H. Sperling; e4# 627, (CNC). 1f: Canada, B.C.; Taylor; larva coll. July 8 '82; F. Sperling; on *Ad*; e4# 439 (CNC). 3f, 6m: Canada, B.C.; Taylor; June 21, 1982; F. Sperling; including e4# 6,7,55,56,59,124,128,395; (British Columbia Provincial Museum: e4# 59[f],124[m]. American Museum of Natural History: e4# 6[m],55[f]. United States National Museum: e4# 56[m], 128[f]. remainder to CNC). 1f, 2m: Canada, B.C.; Taylor; July 8, 1982; F. Sperling; e4# 10,31,140; (CNC: e4# 31[m]. British Museum [Natural History]: e4# 10[m],140[f]). 2f: Clayhurst Ferry, B.C.; larva on *Ad*; Aug. 17 '80; emg. 1981; F.A.H. Sperling; including e4# 117; (CNC: e4# 117[f]. Allyn Museum of Entomology: 1f). 3m: Clayhurst Ferry, British Columbia; larva coll. Aug. 9, 1981; on *Ad*; emg. 1982[2] & 1983[1]; F.A.H. Sperling; including e4# 519, (CNC). 4f, 7m: Canada, B.C.; Clayhurst Ferry; larva coll. Aug. 16 '82; F. Sperling; on *Ad*; emg. 1983; e4# 504,507,508,511–513,515–518,520, (Allyn Museum of Entomology: e4# 507[m]. remainder to CNC). 5m: Alberta, 5 km NW Highland Park; June 14, 1981; F. Sperling; e4# 115,116,676,678,679, (CNC). 5m: Canada, Alberta; Highland Park; 35 km w Fairview; June 9, 1982; F.A.H. Sperling; e4# 41,42,43,44,45, (Alberta Provincial Museum: e4# 41,43. CNC: e4# 42,44,45). 9m: Canada, Alberta; Highland Park; 20 mi. W. Fairview; June 12, 1982; Ted Pike, (CNC). 5m: Canada, Alberta; Highland Park; 20 mi. W. Fairview; June 13, 1982; Ted Pike, (Pike). 1m: Dunvegan, Alberta; larva on *Ad*; Aug. 16, 1980; emg. 1981; F.A.H. Sperling, (CNC). 1f: Canada, Alberta; Dunvegan; June 14, 1981; F.A.H. Sperling, (University of Alberta Strickland Museum). 1f, 2m: Alberta, Dunvegan; June 14, 1981. T. Pike, (Pike). 1f: Canada, Alberta; Dunvegan; larva coll. Aug. 15, 1982; F.A.H. Sperling; on *Ad*; emg. 1983; e4# 438, (CNC). 3m: Canada, Alberta; Dunvegan; June 22, 1982; F.A.H. Sperling; e4# 142,150,547, (University of Alberta Strickland Museum: e4# 150[m]. remainder to CNC). 1f: Dunvegan, Alta.; 30 VI 85; coll. by E.M. Pike; (Pike). 1m: EX OVA; Dunvegan, Alta.; 18 VI 85; coll. by E.M. Pike; (Pike). 4m: 10 mi. S.E. Fairview; Alberta; 17 June 1981; coll. by E.M. Pike; (Pike). 2m: 10 mi. S.E. Fairview; Alberta; 20 & 22 June 1981; coll. by E.M. Pike; (Pike). 1f, 2m: Canada, Alberta; 10 mi. S.E. Fairview; June 22, 1982; Ted Pike; (Pike). 1f: 10 mi. S.E. Fairview; Alta., 20 VI 85; coll. by E.M. Pike, (Pike). 1m: Canada, Alberta; Peace R. area, Camp Island; 22 mi. E. Dunvegan; F.A.H. Sperling; larva on *Ad* on Aug. 15, 1980; [emg. 1981], (CNC). 1f: larva on *Ad*; at Peace R. (town), Alberta; on Aug. 15, 1980; emg. 1981; F.A.H. Sperling; e4# 625, (CNC). 4m: Alberta, Peace River (town); June 10, 1981; F. Sperling (CNC). 2m: Canada, Alberta; Peace River (town); June 13, 1981; F.A.H. Sperling; e4# 114,681, (CNC). 1m: Canada, Alberta; Kleskun Hills; 25 km n.e. Grande Prairie; June 19, 1982; F.A.H. Sperling; e4# 394, (CNC). 1f: Canada, Alberta; Kleskun Hills; e. Grande Prairie; larva coll. Aug. 12 '81; F.A.H. Sperling; on *Ad*; emg. 1983; e4# 437, (CNC).

Derivation of subspecific epithet.— It is a pleasure to name this subspecies after E.M.(Ted) Pike, who has resided in the Peace River region from 1979 to 1985, and has given me much help and encouragement during the past 15 years.

Distinguishing features.— Approximately 75% of individuals of *P. m. pikei* can be correctly distinguished from those of other subspecies of *P. machaon*. Features which distinguish this subspecies are discussed at greater length in the following chapters. Adults of *P. m. pikei* resemble those of *P. m. oregonius* in general maculation and size, but most are distinguished by the more narrow, connected eyespot. *P. m. aliaska* adults resemble those of *P. m. pikei* markedly in maculation, but are separated by larval foodplant, preference for alpine habitat, and smaller size (mean forewing length = 37.5 mm for males, 40.3 mm for females). Though the range of *P. m. pikei* extends in isolated populations to within 25 km of *P. m. aliaska*, at Hudson Hope, there is no evidence of any increased similarity of these two subspecies in the area. *P. m. hudsonianus* adults are separated by preference for boreal forest habitats and a much higher frequency of subdorsal abdominal spots. *P. m. dodi* is easily distinguished from *P. m. pikei* by the greater amount of black scales and hairs, especially on the ventral forewing disc and ventral side of the thorax.

P. m. pikei has the same larval foodplant as the southern subspecies of *P. machaon*, but shares several morphometric and electrophoretic similarities with the northern subspecies. For these reasons, as well as its geographic range, *P. m. pikei* is important in illustrating the

previously unrecognized link between these taxa.

Range.— *P. m. pikei* is composed of a series of populations distributed along approximately 500 km of the Peace River, in northeastern British Columbia and northwestern Alberta. It also occurs at the Kleskun Hills badlands, northeast of Grande Prairie, Alberta. The range of *P. m. pikei* may have once extended farther westward along the Peace River. A specimen in the University of British Columbia collection, which is labelled "Findlay, B.C.", may be from Findlay Forks, 110 km west of Hudson Hope. However, the populations along this part of the Peace River may now be extinct, since it was flooded to form Williston Lake in the late 1960's.

Key to Adults of *P. machaon* Group in Western Canada

The following key is based on color pattern and habitat information. Electrophoretic characters are not used.

1   Black scales on disc of dorsal hindwing (DHW) restricted to basal half (Fig. 2); side of abdomen with broad, yellow, longitudinal band and in some specimens with rounded spots above it (Figs. 6a-d) 2

1′   Black scales extended over more than half of DHW disc (Fig. 3); side of abdomen with only series of square or rounded segmental yellow spots (Figs. 6e-f) 9

2   (1) *All of the following character states*: Black pupil in anal region of DHW connected to margin (Figs. 1a-b,2,3); yellow scales over most of ventral forewing (VFW) disc (Fig. 5A); yellow hairs extended around ventral part of metathorax (Fig. 6a); yellow scales extended over more than 80% of male claspers (Fig. 6a).

          Or no more than one of following: Anal pupil unconnected to margin but flattened and at bottom of red area (Fig. 1C); yellow scales in VFW disc restricted to thick yellow streaks or general flush extended over more than quarter of disc (Fig. 5B); yellow scales extended over only 50–80% of male claspers (Fig. 6b) . . . . . . *P. machaon* Linneaus (Plate 1) 4

2′   Not as above 3

3 (2′) *All of following*: Anal pupil round and centered in red area (Fig. 1D); red and blue areas of anal eyespot more than 3/4 separated by black scales (Figs. 1b,1d,2,3); disc of VFW with at most few thin streaks or light sprinkling of yellow scales (Figs. 5c-e); metathorax with yellow hairs from both sides not in contact ventrally (Figs. 6b-d); without distinct yellow spots above lateral abdominal band (Figs. 6b-c); less than 50% of male claspers covered by yellow scales (Figs. 6c-d).

          Or no more than one of following: Anal pupil large, round and centered if connected to margin (Fig. 2) or small and oval at bottom of red area if unconnected (Fig. 1C); red and blue areas of anal eyespot separated between 1/4 and 3/4 of full width by black scales (Fig. 1C); disc of VFW with thick streaks of yellow or a general flush over less than 1/4 of the disc (Fig. 5B); some distinct yellow spots above lateral abdominal band (Fig. 6d); yellow scales over 50–80% of male claspers (Fig. 6b) . . . .

          . . . . *P. zelicaon* Lucas (Plate 2g-h)

3′   Not as above: most specimens with club-shaped pupil connected to margin;

also most specimens with two or more of character states intermediate between extremes of *P. machaon* and *P. zelicaon* as defined above, rather than combination of extreme states 7

4   (2)   Found near dry grasslands or eroded clay banks in hot habitats; large (FW length usually 40 mm or more in males); forewing apices pointed or not, with distal margin convex or concave; most specimens with yellow scaling of DHW anal cell Cu2 extended close to or beyond divergence of veins Cu1 and Cu2 (Fig. 2: character states 2–4); few specimens with abdomen with spots above lateral band 5

4′   Found in forested boreal regions or on alpine tundra in cool habitats; smaller (FW length usually less than 40 mm in males); forewing apices of most ·specimens rounded, with convex outer margin (Fig. 5A); yellow scaling of DHW anal cell Cu2 in most specimens restricted to distal 1/4 (Fig. 2: character state 1); abdomen with or without yellow spots above lateral band 6

5   (4)   Found in southern and central B.C. Interior, during April to September; anal pupil of eyespot connected to margin in most specimens, but club-shaped rather than flat line; separation between blue and red areas of anal eyespot various; with substantial amount of orange in two or more cells of VHW postmedian band; most specimens with forewing apices pointed, with concave distal margin; (Note: a few summer generation *P. m. dodi* from the southern Alberta and Saskatchewan prairies key out here) .
.... *P. machaon oregonius* (Edwards) (Plate 1g-h)

5′   Found in Peace River region of northeastern B.C. and northwestern Alberta, during June and early July; anal pupil of many specimens flat rather than club shaped; most specimens with very little black separation between red and blue in anal eyespot; most specimens with substantial amounts of orange in only one or no cell of the VHW postmedian band; forewing apices pointed or rounded ....
.... *P. machaon pikei* Sperling (Plate 1e-f)

6   (4′)   Found in Alaska, Yukon, western Northwest Territories, and northern British Columbia, most specimens on alpine tundra; DHW anal pupil in form of thin line, at bottom of red area, and connected to margin (Fig. 1A); red and blue areas of anal eyespot with no or very little black separation (Fig. 1A); no spots or in few specimens one or two spots on abdomen above lateral band .... *P. machaon aliaska* Scudder (Plate 1a-b)

6′   Found in boreal forest from Alberta to northern Quebec; DHW anal pupil in most specimens club shaped; red and blue areas of anal eyespot separated or not by black scales; at least one yellow spot above lateral abdominal band in most specimens .... ;.....
.... *P. machaon hudsonianus* Clark (Plate 1c-d)

7   (3′)   Found near dry grassland or eroding clay banks in hot prairie habitats of southern Alberta or Saskatchewan; anal pupil of DHW club-shaped and connected to margin; forewing apex of many specimens pointed, with concave distal margin; hindwing tails of many specimens long, slightly narrowed in middle and curved (Fig. 2); yellow scales in DHW anal cell

Cu2 extended or not beyond divergence of veins Cu1 and Cu2 (Fig. 2: character states 3–4); no distinctly separated yellow spots above lateral abdominal band ....*P. machaon dodi* McDunnough (Plate 2a-b)

7′   Found in broad range of habitats, but most in southern zones of boreal forest; anal pupil of DHW varied; forewing apex of most specimens rounded, and distal margin straight or rounded; hindwing tails of medium or short length, straight and not constricted in middle (Fig. 3); yellow scales of distal hindwing cell Cu2 in most specimens restricted to distal quarter; less than five yellow spots above lateral abdominal band .... yellow morph hybrids 8

8 (7′) Found in Manitoba or eastern Saskatchewan *and* with one or more of the following character states: anal pupil on DHW round and centered; disc of VFW with at most light sprinkling or thin streaks of yellow scales; thorax with yellow hair not in contact ventrally and no yellow hairs on ventral midline of first two abdominal segments; male claspers covered over less than 50% of surface by yellow scales ....*P. machaon X polyxenes*

8′   Found in western Saskatchewan and westward, with any of the following combinations:

A. In predominantly forested habitats and with club shaped, connected pupil.

or **B.** Specimen with between two and five of the following six character states: 1, DHW anal pupil connected to margin or unconnected, flattened and at bottom of red area; 2, Blue and red areas of anal eyespot not separated by black along at least 1/4 of boundary; 3, disc of VFW with yellow scales or thick streaks over at least 1/4 of area; 4, metathorax with yellow hair meeting ventrally; 5, one to five distinct spots above lateral abdominal band; 6, yellow scales over more than 50% of male claspers ... . *P. zelicaon X machaon* (Plate 2c-f)

9 (1′) Found in southern and central Manitoba or southeastern Saskatchewan; postmedian band of VHW with substantial amounts of orange in at least two cells, and all cells in most specimens; distinct yellow spots in two subdorsal rows on at least five and in most specimens on all segments of abdomen.................................... 10

9′   Found in southwestern Saskatchewan and south or central Alberta; postmedian band of VHW with substantial amounts of orange in less than six cells (only two or three in most specimens); distinct yellow spots in subdorsal position on abdomen usually absent on at least 2 segments 11

10 (9) Anal pupil of DHW unconnected to margin or club shaped if connected; blue and red areas of anal eyespot fully separated by band of black scales; less than half of hairs on tegula yellow; yellow scales in apical cell of postmedian band of VFW varied; postmedian band of VHW with orange in all eight cells; lower half of side of abdomen with rounded yellow spot on each abdominal segment; yellow spots in subdorsal position on abdomen absent on no more than two segments; less than 10% of male claspers covered by yellow scales; females with markedly reduced postmedian band on DHW, compared to males ....*P. polyxenes asterius* Stoll (Plate 3g-h)

10' *All three of following character states*: anal pupil club-shaped and
      connected to margin; more than 50% of hairs on tegula yellow; apical cell
      of VFW postmedian band with distinct patch of yellow, but occupying less
      than half of cell area;
      or one or more of the following character states: anal pupil thin line at
      lower edge of red area, connected to margin; blue and red areas of anal
      eyespot not completely separated by black scales; apical cell of VFW
      postmedian band more than 50% covered by yellow scales; postmedian
      band of VHW with no orange in at least one cell; large square spots or
      broad band of yellow along lower half of abdomen; yellow spots in
      subdorsal position on abdomen absent from at least three segments; more
      than ·10% of male claspers covered by yellow scales; females with
      postmedian band on DHW same width as on males . . . .
      . . . . *P. polyxenes X machaon* (Plate 3d)
11 (9') Anal pupil of DHW round and centered in red area; blue and red areas of
      anal eyespot fully separated by black scales; male claspers with less than
      10% yellow scales . . . . black morph of *P. zelicaon* (Plate 3a)
11' One or more of following character states: anal pupil of DHW connected to
      margin or low and oval if unconnected; blue and red areas of anal eyespot
      of DHW not separated by black scales along at least 1/4 of boundary; male
      claspers with more than 10% yellow scales 12
12 (11') Found near dry grassland or eroding clay banks in hot prairie habitats . . .
      . . . . black morph of *P. machaon dodi*
12' Found in predominantly forested habitats . . . .
      . . . . black morph of *P. zelicaon X machaon* (Plate 3b-c)

MORPHOMETRIC AND ELECTROPHORETIC CHARACTERS

Characters of Adults

Only a few species within the *Papilio machaon* group are easy to distinguish on the basis of morphometric characters. The most divergent of these is *P. alexanor* Papilio, which has a striped wing pattern and male genitalia unlike the other species of the group (Higgins, 1975), but shares with them an apotypic (derived) larval color pattern and larval foodplant. Diagnostic interspecific distinctions in genitalia are also found in *P. indra* and *P. hospiton*. The remaining five species in the *P. machaon* group are much more similar with respect to adult characters.

The character states traditionally used by systematists to distinguish among *P. machaon*, *P. zelicaon* and *P. polyxenes* are especially difficult to employ, because the variation in color pattern in any one species is paralleled by the other species in other areas. Also, virtually no character states stand on their own, without consideration in combination with other characters. For this reason, I use multivariate statistical methods to provide more reliability in clustering groups of similar individuals, both at the level of populations and species. As well, two character suites were surveyed and compared: one, the traditionally employed color pattern data; and two, new information about enzyme alleles.

Cluster resolution with principal components analysis.— Three principal components analyses (PCAs) were applied to the same 728 individuals using, respectively, morphometric data, electrophoretic data, and both data sets combined. All PCAs gave generally similar orientations of locality samples (Figures 7 and 8).

These samples were then compared with samples from or near the type localities of named populations, which were scored with factor loadings derived from analysis on morphometric data alone (Figure 9). From this comparison, it was clear that in all three principal components analyses the first axis separated most yellow morph populations of *Papilio machaon* (No. 1,2,3,5,12,13,15) from *Papilio zelicaon* (No. 8,9,10,16,17a,18,19), the second axis separated *Papilio polyxenes* (No. 11,17b,20) from the previous two groups and the third axis provided a partial separation of the *P. machaon* cluster. Factor loadings for all three PCAs are included in Tables 12 and 13.

Electrophoretic characters showed a close association between (*P. m. dodi* Figure 7, No. 5) and other *P. machaon* subspecies, while morphometric characters (Figure 8 and 9) indicated a more intermediate position for *P. m. dodi* between *P. zelicaon* and other *P. machaon* subspecies. Populations from the Alberta foothills, such as Bragg Creek, were intermediate in both electrophoretic and morphometric characters. *P. m. oregonius* populations, which have not previously been associated with *P. machaon* in most publications, showed a close association with *P. machaon* on the basis of both character suites.

Although the second axis of each of the three PCAs served to separate *P. polyxenes* from both *P. machaon* and *P. zelicaon*, the black morphs associated with populations of predominantly yellow individuals were placed in an intermediate position between them in those analyses which included morphometric data. Electrophoretic characters showed a much closer association between the black and yellow morphs of most populations. The sample size from central Manitoba (No. 14) was relatively small; nonetheless, the single yellow morph specimen showed a close association with *P. machaon* for both character types. The black samples from central Manitoba showed a somewhat closer association with *P. machaon* than with *P. polyxenes* on the basis of electrophoretic characters, and grouped closely with *P. polyxenes* in morphometric characters.

Although plotting entire population samples on the principal component axes served to group most of these with either *P. machaon*, *P. zelicaon* or *P. polyxenes*, the associations of a number of intermediate samples were uncertain. In particular, this procedure did not distinguish between samples which were intermediate because the whole population was intermediate, and samples which contained a mixture of individuals of more than one of the above species. To facilitate such a distinction, the scores of all the individuals within a region or at a locality were plotted as frequency histograms on principal component axes (Figures 12–13). Since there seemed to be regional trends with respect to the frequency of intermediate individuals, the total sample used in the original PCAs was divided into five major regions (Figure 10).

Both morphometric and electrophoretic characters provided a good separation of *P. machaon* from *P. zelicaon* in southern and central British Columbia, as well as in the Peace River region (Figure 12). The few specimens which were intermediate on the basis of either character type grouped with *P. zelicaon* when both character types were considered together. The sample from southern Alberta and Saskatchewan showed a reasonable degree of clustering on the basis of electrophoretic but not morphometric characters, and the low frequency section between these two clusters was shifted toward *P. zelicaon*, with both character suites considered simultaneously.

With samples from the southern Alberta and Saskatchewan region considered separately, it was clear that the frequencies of *P. machaon* and *P. zelicaon* differed markedly by locality (Figure 11 and 15). Specimens collected along high river banks were likely to be more similar

Plate 1. Color pattern of *P. machaon* subspecies. Each specimen has dorsal and ventral views of right wings figured on right and left sides, respectively: a, *P. m. aliaska*, male Mi. 391, Alaska Hwy., British Columbia, July 2, 1972; b, *P. m. aliaska*, female Pink Mountain, British Columbia, *Ex* larva, coll. 17 Aug. 1982, on *Artemisia arctica; c, P. m. hudsonianus*, male Thompson, Manitoba, July 2, 1983; d, *P. m. hudsonianus*, female 25 km NE of The Pas, Manitoba, June 14, 1980; e, *P. m. pikei*, male 7 km NE of Hudson Hope, British Columbia, *Ex* larva, coll. 20 Aug. 1984, on *Artemisia dracunculus*; f, *P. m. pikei*, female Dunvegan, Alberta, June 14, 1981; g, *P. m. oregonius*, male Kamloops, British Columbia, *Ex* larva, coll. 27 Aug. 1983, on *Artemisia dracunculus*; h. *P. m. oregonius*, female Kamloops, British Columbia, *Ex* larva, coll. 27 Aug. 1983, on *Artemisia dracunculus*.
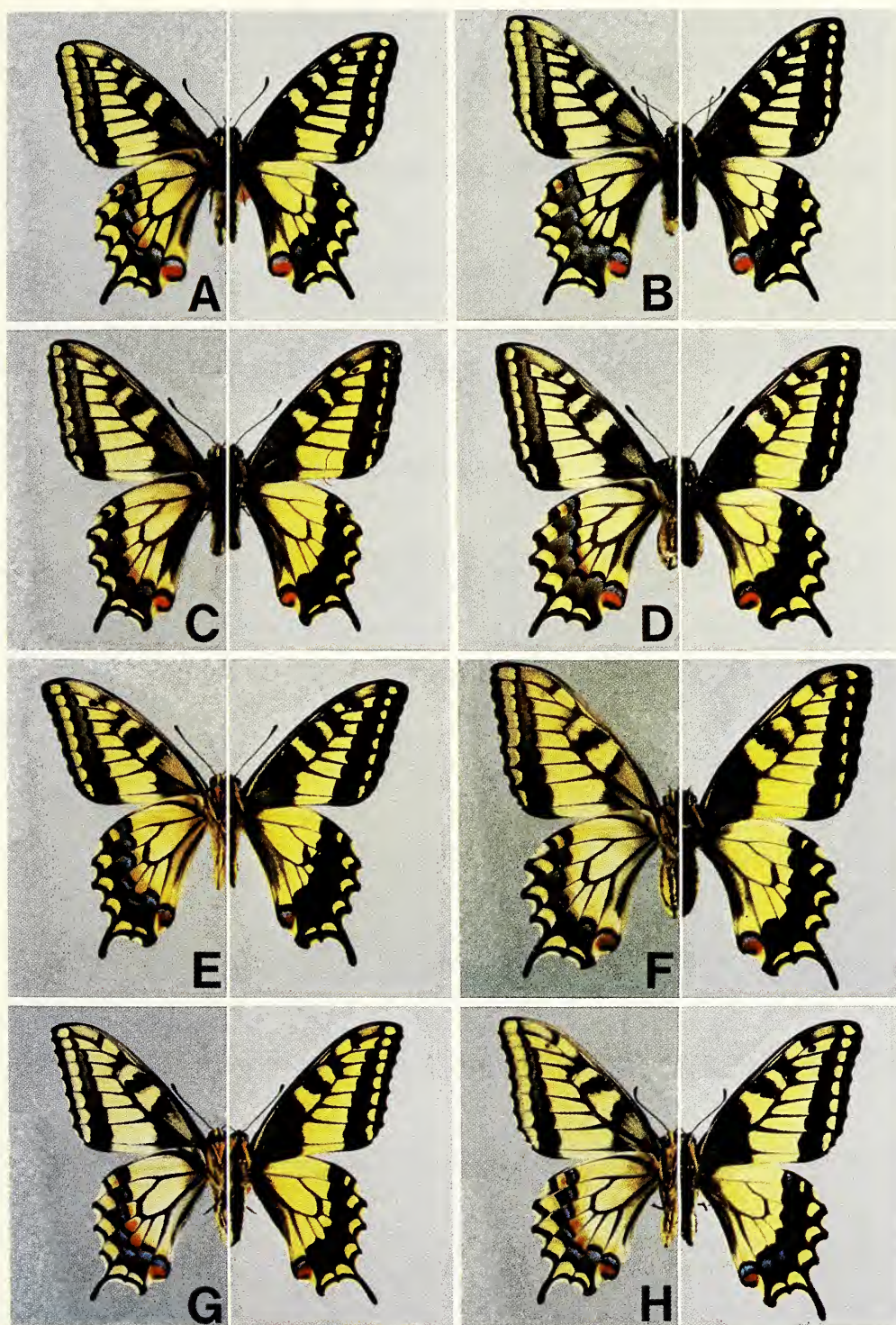
Plate 2. Color pattern of *P. machaon, P. zelicaon* and hybrids Each specimen has dorsal and ventral views of right wings figured on right and left sides, respectively. Figure h is reversed and shows left wings: a, *P. m. dodi*, male 11 mi. N of Taber, Alberta, *Ex* larva, coll. 19 Aug. 1981, on *Artemisia dracunculus*; b, *P. m. dodi*, female Drumheller, Alberta, *Ex* larva, coll. 22 July 1981, on *Artemisia dracunculus*; c, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, *Ex* larva, coll. 18 July -7 Aug. 1982, on *Zizia aptera*; d, *P. zelicaon* X *machaon*, female Bragg Creek, Alberta, *Ex* larva, coll. 18 July -7 Aug. 1982, on *Zizia aptera*; e, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, May 31, 1980; f, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, May 31, 1980; g, *P. zelicaon*, male Wintering Hills, 18 km S Drumheller, Alberta. May 24, 1982; h, *P. zelicaon*, female Waterton Park, Alberta. *Ex* larva, coll. 19 Aug. 1981, on *Lomatium dissectum*.
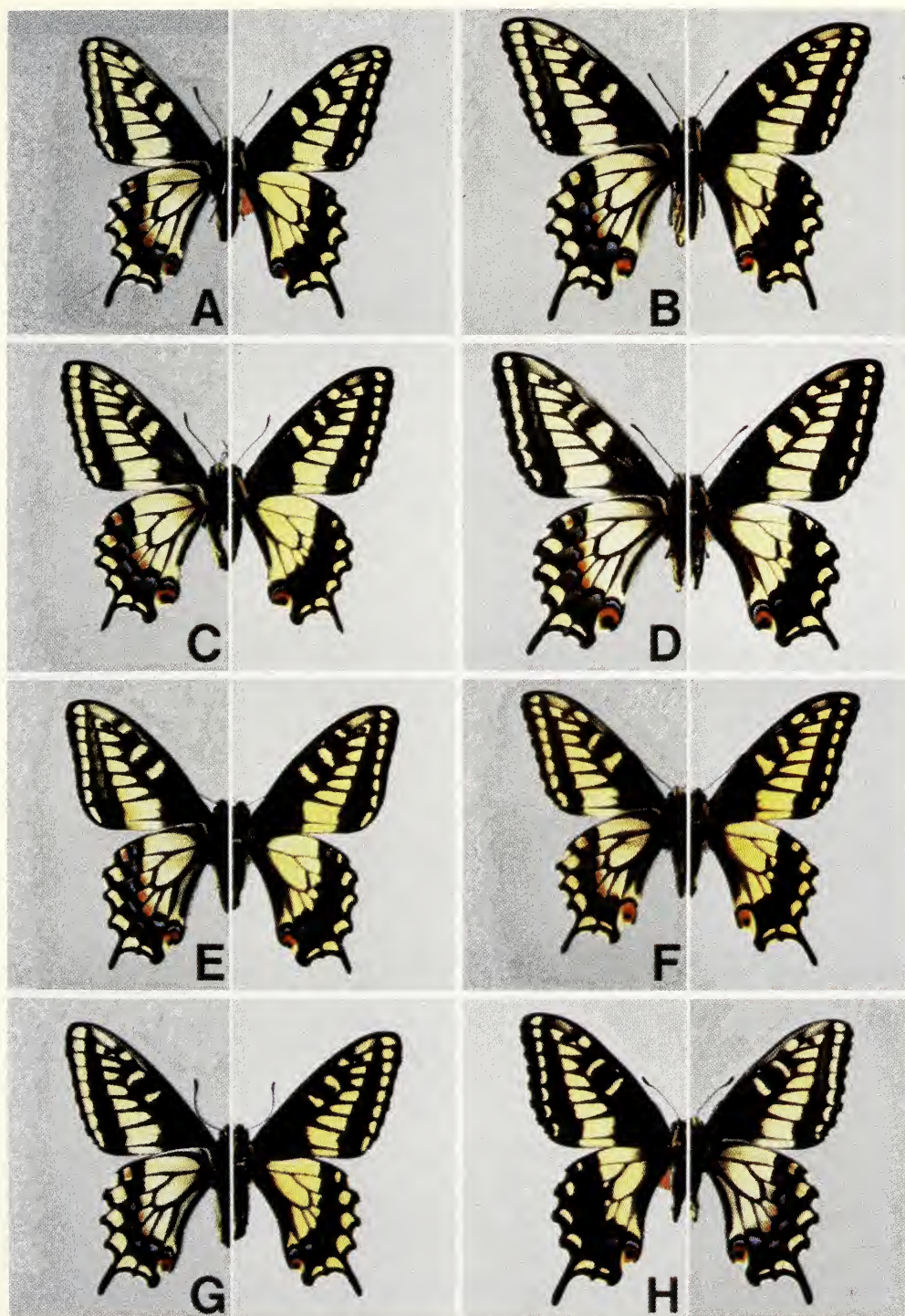
Plate 3. Color pattern of dark morphs of *P. machaon* group species. Each specimen has dorsal and ventral views of right wings figured on right and left sides, respectively: a, *P. zelicaon*, male Wintering Hills, 18 km S of Drumheller, Alberta, May 30, 1982; b, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, *Ex* larva, coll. 15 July -7 Aug. 1982, on *Zizia aptera*; c, *P. zelicaon* X *machaon*, male Bragg Creek, Alberta, June 23, 1974; d, *P. polyxenes* X *machaon*, female Duck Mountain Park, Manitoba, *Ex* larva, coll. 25 June 1980, on *Zizia aptera*; e, *P. m. bairdii*, male Sunset Crater, E of Flagstaff, Arizona, May 5, 1980; f, *P. m. bairdii*, female Flagstaff, Arizona, May 27, 1980; g, *P. p. asterius*, male Burlington, Ontario, *Ex* larva, coll. Aug. 1981, on garden carrot; h, *P. p. asterius*, female Burlington, Ontario, *Ex* larva, coll. Aug. 1981, on garden carrot.
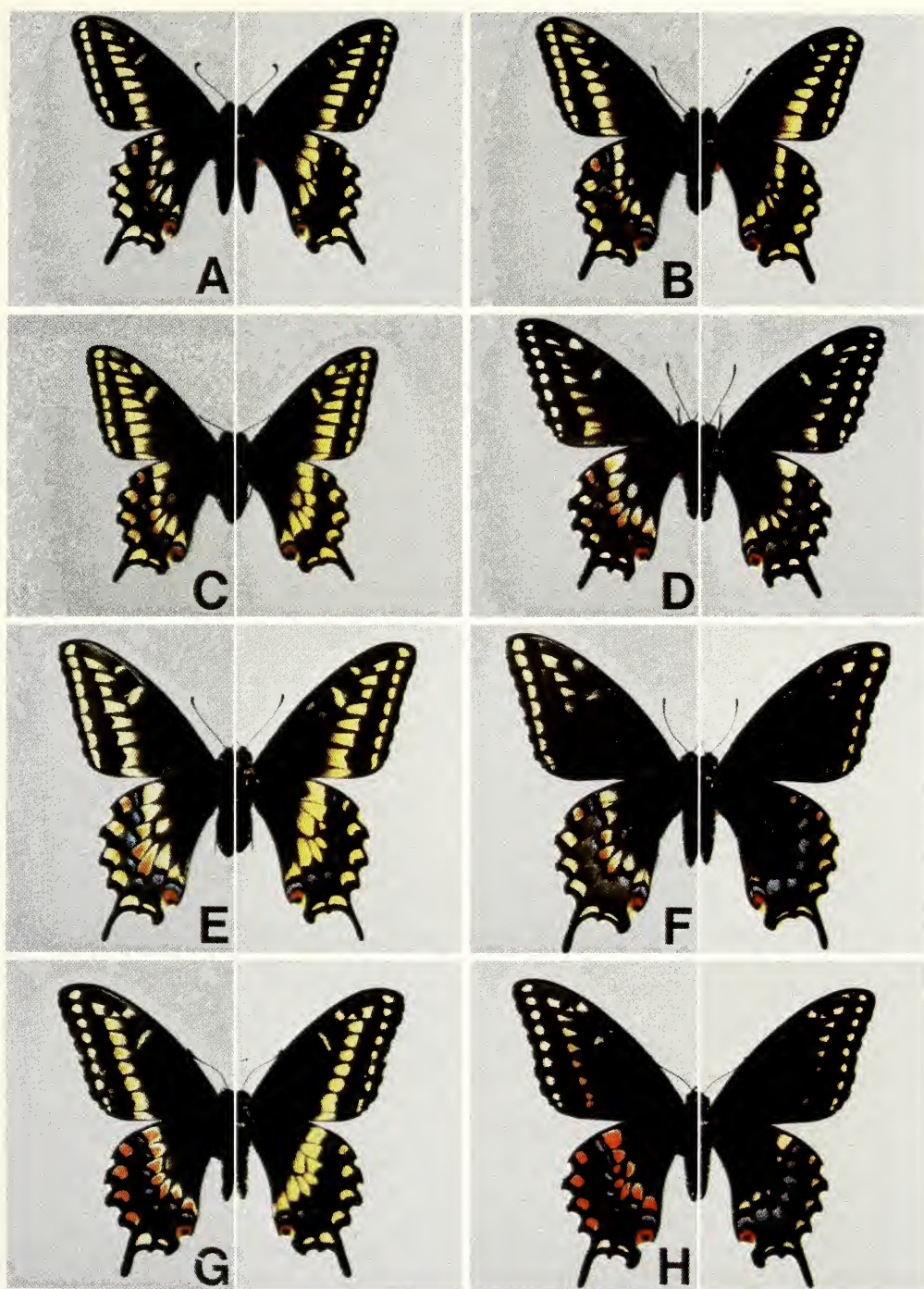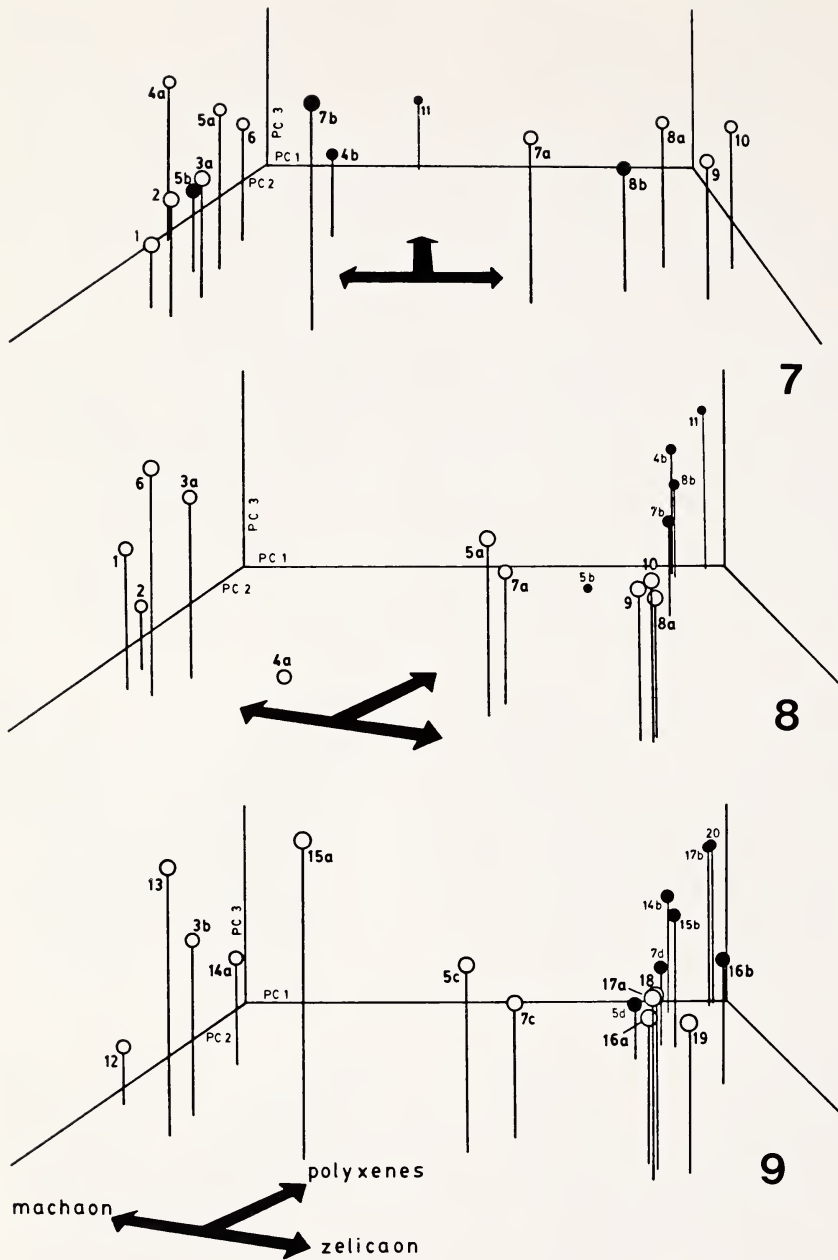
Figures 7 to 9. Mean scores of representative populations plotted on first three principal component axes. See Table 4 for key to locations. Black circles indicate black morph adults, and empty circles indicate yellow morph adults. PC 1, PC 2 and PC 3 refer to the first, second and third principal component axes. Figure 7. 3D.PCA on electrophoretic data alone Populations include only individuals used in the original analysis. Figure 8. 3D.PCA on morphometric data alone Populations include only individuals used in the original analysis. Figure 9. Additional samples scored with morphometric loadings. Populations are partly or completely composed of individuals not included in original analysis, but scored with factor loadings from PCA on morphometric data alone. Most populations are either topotypic or from close to type localities.

Table 4. Population samples of the *P. machaon* species group used in Figures 7–9.

Letter after taxon name indicates yellow color morph (Y) or black color morph (B).

No. in figs.	Locality and region	Sample size	Taxon and color morph
1.	Clayhurst Fy., Peace R. area, British Columbia	20	*P. m. pikei*
2.	Pink Mt., northern British Columbia	36	*P. m. aliaska*
3a.	Thompson, northern Manitoba	37	*P. m. hudsonianus*
3b.	Thompson, northern Manitoba	46	*P. m. hudsonianus* (expanded sample)
4a.	Duck Mt. Park, central Manitoba	1	*P. machaon X polyxenes* -Y
4b.	Duck Mt. Park, central Manitoba	7	*P. polyxenes X machaon* -B
5a.	Drumheller, southern Alberta	79	*P. m. dodi* -Y
5b.	Drumheller, southern Alberta	2	*P. m. dodi* -B
5c.	Drumheller, southern Alberta	105	*P. m. dodi* -Y (expanded sample)
5d.	Drumheller, southern Alberta	3	*P. m. dodi* -B (expanded sample)
6.	Kamloops, southern British Columbia	48	*P. m. oregonius*
7a.	Bragg Creek, south-central Alberta	65	*P. zelicaon X machaon* -Y
7b.	Bragg Creek, south-central Alberta	7	*P. zelicaon X machaon* -B
7c.	Bragg Creek, south-central Alberta	160	*P. zelicaon X machaon* -Y (expanded sample)
7d.	Bragg Creek, south-central Alberta	44	*P. zelicaon X machaon* -B (expanded sample)
8a.	Wintering Hills - West, southern Alberta	17	*P. zelicaon* -Y
8b.	Wintering Hills - West, southern Alberta	3	*P. zelicaon* -B
9.	Thunder Mt., northern British Columbia	23	*P. zelicaon*
10.	Vancouver area, southern British Columbia	10	*P. zelicaon*
11.	Caledonia, southern Wisconsin	15	*P. p. asterius*
12.	Steese Hwy., central Alaska	39	*P. m. aliaska*
13.	The Dalles area, northern Oregon	8	*P. m. oregonius*
14a.	Riding Mt. Park, central Manitoba	33	*P. m. hudsonianus* and *P. polyxenes X machaon* -Y
14b.	Riding Mt. Park, central Manitoba	32	*P. p. asterius* and *P. polyxenes X machaon* -B
15a.	Salida Co., southern Colorado	9	*P. m. bairdii*-Y
15b.	Salida Co., southern Colorado	17	*P. m. bairdii*-B
16a.	Judith Mts., central Montana	10	*P. zelicaon* -Y
16b.	Judith Mts., central Montana	8	*P. zelicaon* -B

Table 4 (continued)

No. in figs.	Locality and region	Sample size	Taxon and color morph
17a.	Jefferson Co., northern Colorado	19	*P. zelicaon* -Y
17b.	Jefferson Co., northern Colorado	24	*P. p. asterius* -B
18.	Gothic, central Colorado	25	*P. zelicaon* -Y
19.	San Francisco area, central California	27	*P. zelicaon*
20.	Ottawa to Point Pelee, Ontario	59	*P. p. asterius*

to *P. machaon* from other regions, especially in electrophoretic characters. Specimens from prairie hilltops were more likely to belong to *P. zelicaon*. This situation was well illustrated by the locality samples from the Drumheller region. The sample from the river bank just above the town of Drumheller contained only *P. m. dodi* and a few intermediate specimens. There were mostly *P. zelicaon* in the samples from the Hand Hills and the western part of the Wintering Hills, which are about 15 and 12 km, respectively, from the nearest deeply cut river valleys or ravines. A mixture of both species was at a hilltop on the eastern part of the Wintering Hills, about 4 km from the nearest deep ravine and 6 km from the banks of the Red Deer River.

This pattern was basically the same as that in southern British Columbia, where *P. m. oregonius* lives in the dry grassland habitats of the central Interior, while *P. zelicaon* is far more common in forested and wetter habitats. In the Peace River region *P. m. pikei* also tended to occur on the dry river banks and *P. zelicaon* on the hills farther away from the river. However, an added complication is that another subspecies, *P. m. aliaska*, frequents the boreal and especially the alpine regions of northern British Columbia, north of the Peace River.

In the predominantly forested regions of central Alberta, there seemed to be a different sort of relationship between *P. machaon* and *P. zelicaon* (Figure 11 and 14). At the northern localities (Marten Mt. to Adams Lkt.) there was a predominance of electrophoretic and morphometric character combinations which tended to resemble *P. zelicaon*, as well as a significant proportion of more intermediate individuals. However, a few individuals were indistinguishable from northern *P. machaon* even with the two character types considered together, and it was unclear whether these formed a distinctive group from the others. In the more southerly localities (Buck Lk. to Bragg Cr.), the different phenotypes evident in the north tended to merge even more. Populations from single localities were composed of a few individuals indistinguishable from either *P. machaon* or *P. zelicaon*, but the majority was intermediate. There was a single peak near the midpoint between the two extremes, which tapered off to either side. The different phenotypes all occurred within the same habitat as well. Though electrophoretic and morphometric characters showed a generally concordant pattern, electrophoretic character combinations were more obviously intermediate than were morphometric characters.
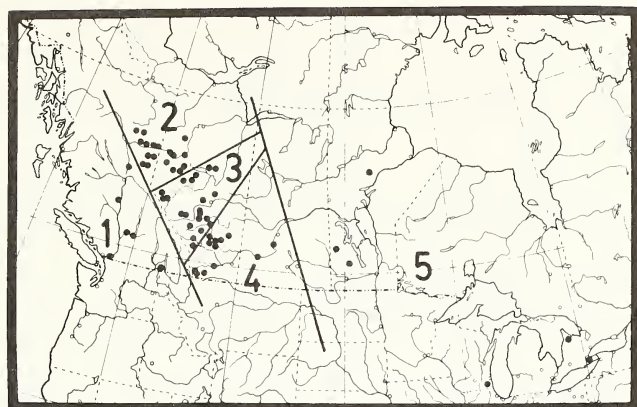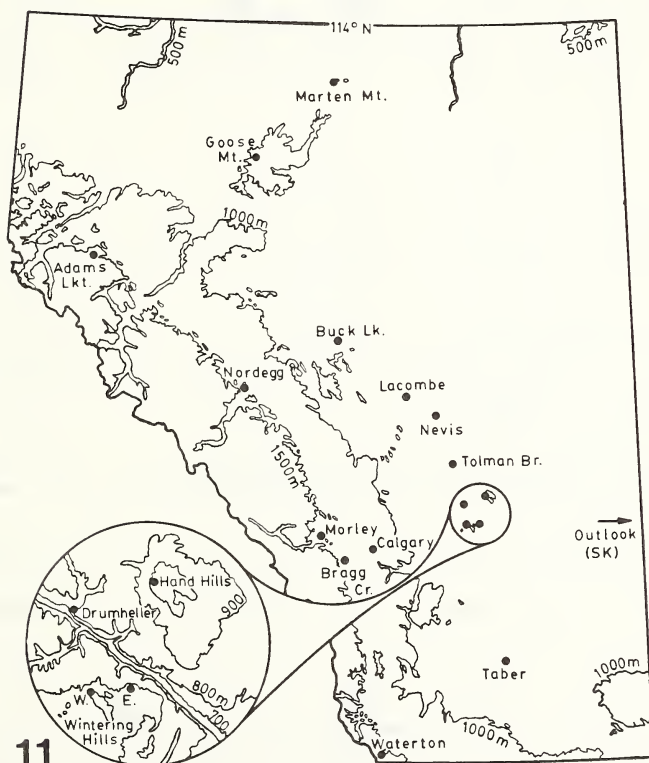
Figures 10 and 11. Figure 10. Western Canada, showing 5 major regions: 1, southern and central British Columbia (s+cent. BC); 2, Peace River region (Peace R.); 3, central Alberta (cent. AB); 4, southern Alberta and Saskatchewan (s AB+SK); 5, Manitoba and eastward (MB+east). Dots show localities from which specimens were used in the initial PCAs. Figure 11. Central and southern Alberta, with major localities. Localities refer to those used in figures 14 and 15.
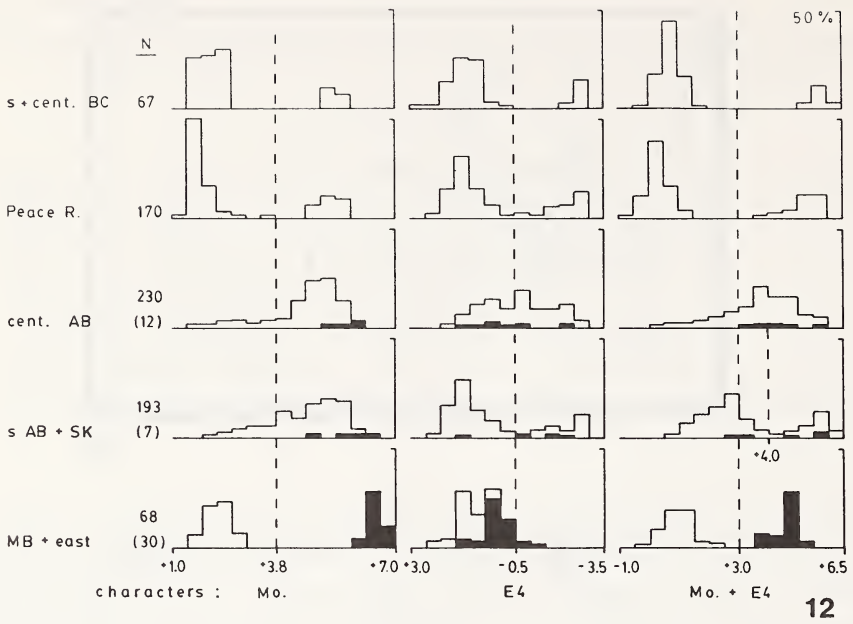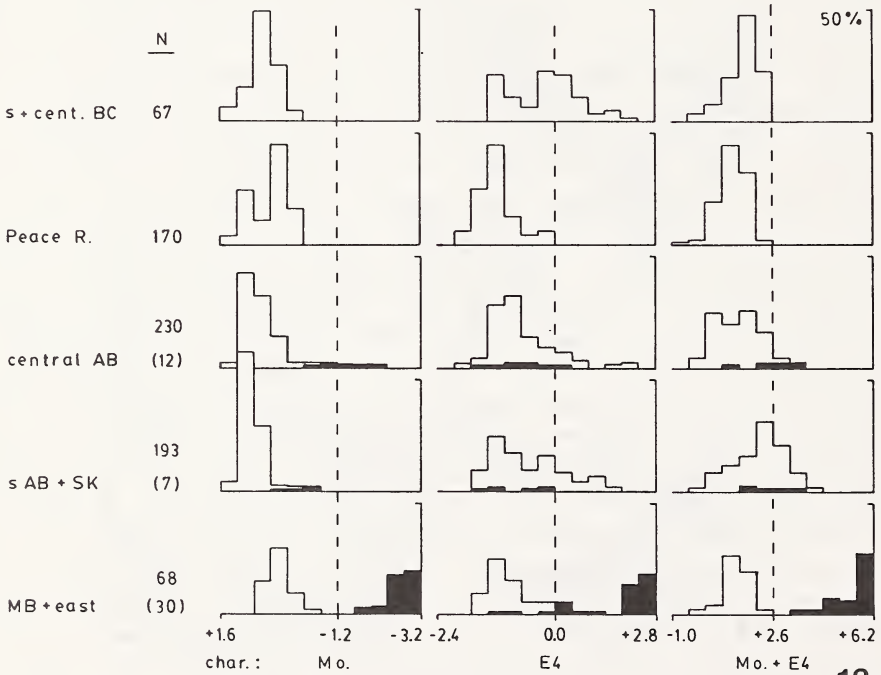
Figures 12 and 13. Component axes of three separate PCAs, with frequency histograms of all individuals in each of five major geographic regions (see Figure 10). Only specimens used in original PCAs are included. Darkened portions of histograms indicate black morphs. Dashed lines indicate divisions between taxa. Mo. = morphometric characters. E4 = electrophoretic characters. Figure 12. First component axes, by major region Figure 13. Second component axes, by major region
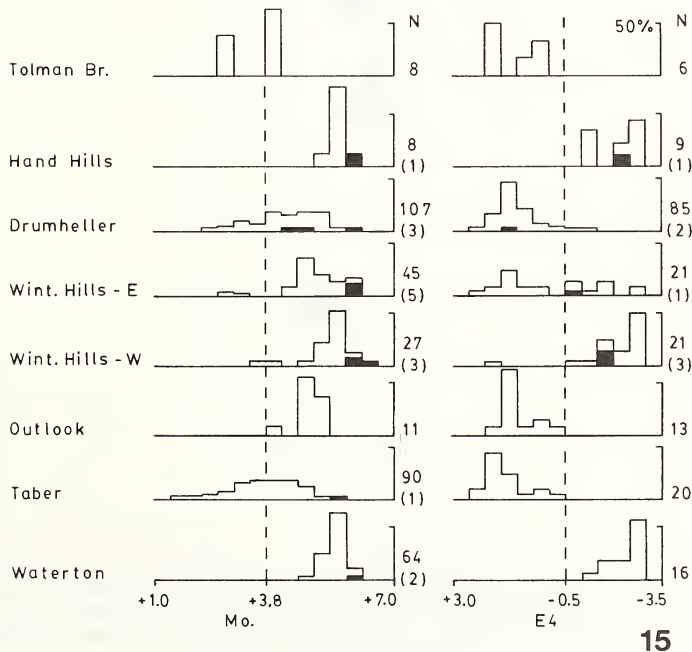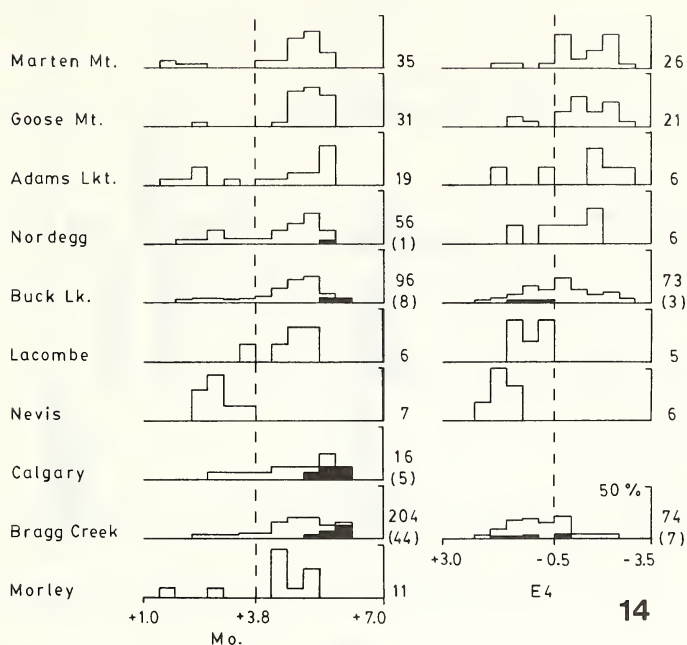
Figures 14 and 15. Locality samples plotted on first component axes. Some samples include individuals not used in original PCAs. Darkened parts of histograms indicate black morphs. Dashed lines indicate divisions between taxa. Mo. = morphometric characters. E4 = electrophoretic characters. Figure 14. Central Alberta samples plotted on PC.1. Figure 15. Southern Alberta and Saskatchewan samples on PC.1.
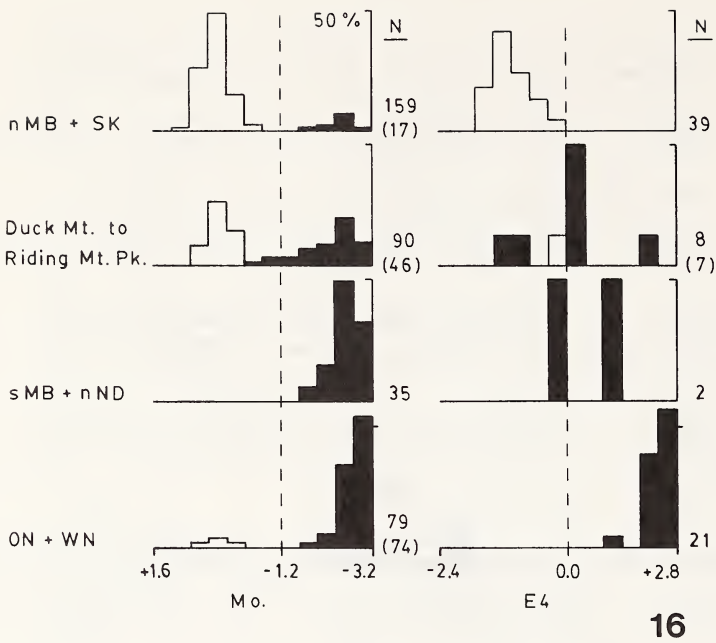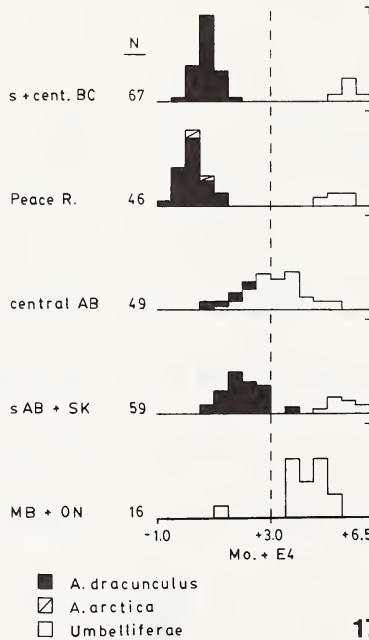
Figures 16 and 17. Dashed lines indicate divisions between taxa. Mo.= morphometric characters. E4 = electrophoretic characters. Figure 16. Area samples from Manitoba and eastward. Samples are plotted on second component axes, and some include individuals not included in original PCAs. Black morph individuals are indicated by darkened portions of histograms. Geographic areas: n MB + SK = northern Manitoba and northern Saskatchewan; Duck Mt. to Riding Mt. Pk. = Duck Mountain and Riding Mountain Parks; s MB + n ND = southern Manitoba and northern North Dakota; ON + WN = Ontario and Wisconsin. Figure 17. Adults reared from wild-collected larvae Histogram key: darkened = larvae on *Artemisia dracunculus*; cross-hatched = on *Artemisia arctica*, clear = on umbelliferous larval hostplants. Individuals are plotted on first component axis of PCA on combined character set and include only those used in original PCA. Regions refer to those indicated in Figure 10.
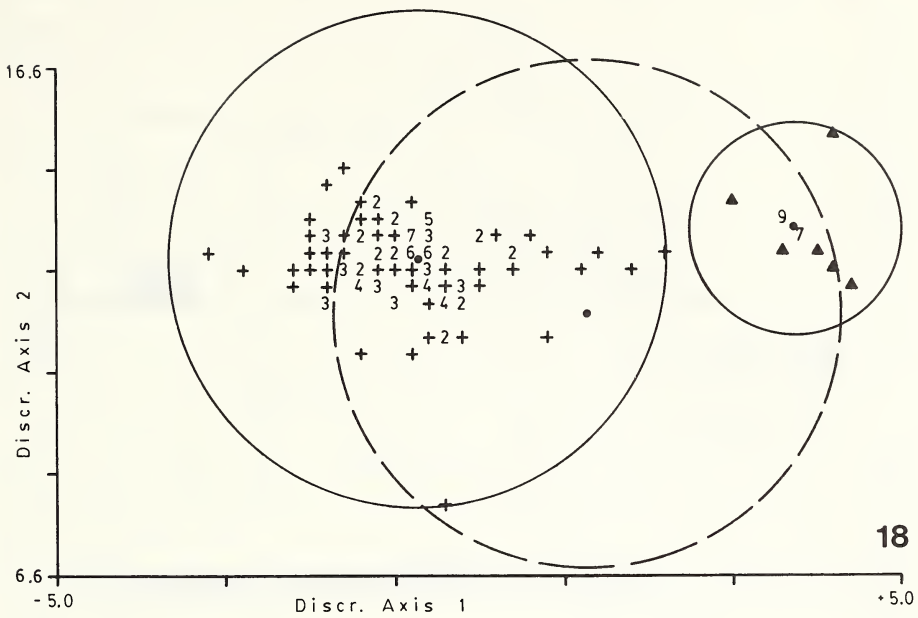
Figures 18 and 19. Reared adults plotted on discriminant axes, including only those used in original discriminant analyses. Numbers indicate more than one data point with the same coordinates. Circles indicate maximum diameters of the three original groups. Dashed lines indicate locations of populations from opposite figure. Figure 18. 2D.DFA plot of reared samples: southern Alberta. On *A. dracunculus* (+) N=119; on umbellifers (triangles) N=22. Figure 19. 2D.DFA plot of reared samples: central Alberta. Only umbellifer-reared individuals shown, N=45.
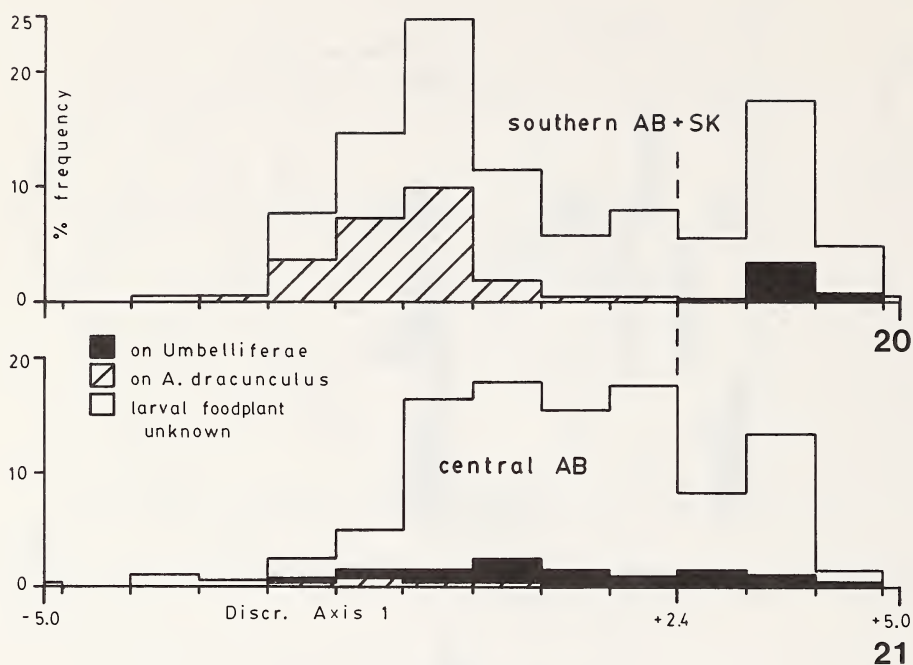
Figures 20 and 21. All adults from central and southern Alberta (AB), and southern Saskatchewan (SK), plotted on first discriminant axis. Reared individuals are indicated as subsets. Figure 20. All southern Alberta and Saskatchewan specimens, plotted on DFA.1 N=497, including N=119 reared from *A. dracunculus* and N=22 reared from umbellifers.

Figure 21. All central Alberta specimens, plotted on DFA.1 N=481, including N=7 reared from *A. dracunculus* and N=45 reared from umbellifers.

The most *P. machaon*-like individuals from the southern foothills of Alberta had morphometric character combinations more similar to *P. m. hudsonianus* than to *P. m. dodi*. In fact, no specimens were collected on the southern prairies which were as *P. m. hudsonianus* or *P. m. aliaska*-like as a few individuals taken at Bragg Creek and Buck Lake, localities geographically close to *P. m. dodi* populations. This suggests that the hybrid populations are at least partly a product of hybridization between *P. zelicaon* and the more northerly *P. machaon* races, rather than with *P. m. dodi*. On the other hand, most of the specimens from these two localities tended to be very similar to *P. m. dodi* in morphometric characters, while most were more intermediate between *P. zelicaon* and *P. machaon* in electrophoretic characters. This suggests that the very similar wing and body color pattern combinations which occur in both *P. m. dodi* and the hybrid swarms may have arisen in different ways.

In Alberta, the morph with black wings occurred together with the more common yellow members of both *P. machaon* and *P. zelicaon*. The former specimens had a range of electrophoretic character combinations matching the remainder of the population with which they occurred. This applied to individuals collected with other *P. zelicaon* specimens on prairie hilltops, the intermediate hybrid populations of the Alberta foothills, and the *P. m. dodi* collected along dry river banks. On this basis it appears as though this morph has become a

regular part of all of these populations. Although the color pattern of the black morph in many respects resembles that of *P. p. asterius*, there was no good electrophoretic evidence of hybridization with *P. polyxenes* in these populations.

The situation in Manitoba was far less clear (Figure 16), though there probably are hybrid swarm populations in this region as well. These hybrid populations appear to be the result of interactions between *P. machaon* and *P. polyxenes*, rather than between *P. machaon* and *P. zelicaon* as in central Alberta. The dramatic effect of the gene for the black wing morph made it more difficult to demonstrate phenotypic intermediacy in morphometric characters, and I was able to subject only a small number of individuals from central Manitoba to electrophoretic analysis. However, populations scored on the second PC axis tended to be intermediate in electrophoretic characters. Also a sizable proportion of black morph individuals in central Manitoba tended to take on character states found in *P. machaon*. For example, most had a club-shaped anal pupil and many had more yellow on the tegulae and apical forewing cell than in *P. p. asterius* from southern Ontario or the United States.

Adult characters versus larval foodplants.— Separation of *P. machaon* from *P. zelicaon* and *P. polyxenes* on the basis of electrophoretic and morphometric characters was supported by a comparison of larval foodplants. Scores of adults reared from larvae collected on *Artemisia* were plotted against those of individuals from various species of Umbelliferae, on the first PC axis derived from both the electrophoretic and the morphometric characters combined (Figure 17). In the Peace River region, individuals reared on *Artemisia arctica* from alpine habitats grouped with those reared on *Artemisia dracunculus* from dry, grassy river banks. The *P. machaon* from southern Alberta and Saskatchewan, reared on *A. dracunculus*, were also separated from *P. zelicaon* on this basis, although their more similar morphometric characters resulted in a somewhat closer grouping. The single *P. machaon*-like individual reared from central Manitoba was obtained on an umbellifer.

The specimens reared on *A. dracunculus* from central Alberta were collected at Nevis Junction, on a northward extension of prairie habitat along the Red Deer River. These adults resembled those of *P. m. dodi* from further south along the river and were undoubtedly just an outlying population of this race. They also, however, resembled some specimens collected on umbellifers farther to the west. Larvae of the hybrid populations from central Alberta feed on umbellifers, and in this respect are similar to *P. zelicaon*. Reared material showed the same wide range of phenotypes as the wild- collected adults.

Since PCAs on the total sample from western Canada provided only a partial separation between *P. machaon* and *P. zelicaon* from central and southern Alberta on the basis of morphometric characters, I attempted to improve the separation with discriminant factor analysis (DFA) of foodplant groups. Three foodplant groups were defined. The first included all specimens reared from *A. dracunculus* in either southern or central Alberta. The second included all material from umbellifers in the southern Alberta region, all of which were from *Angelica*, *Lomatium* or *Heracleum* in the Waterton Park and Crowsnest Pass area. The third group included all the adults reared from umbellifers in the central Alberta region. The morphometric characters used in this analysis were the same as those used in the PCAs, except that only 10 characters were used because one character (tegula color) showed no variation in the groups defined above. The discriminant axis loadings are included in Table 12.

As with the PCAs on electrophoretic characters, the DFA gave a fairly good separation of *P. machaon* and *P. zelicaon* in southern Alberta (Figures 18–19). However, the umbellifer feeders from central Alberta did not separate very well from either of the other two groups. With all
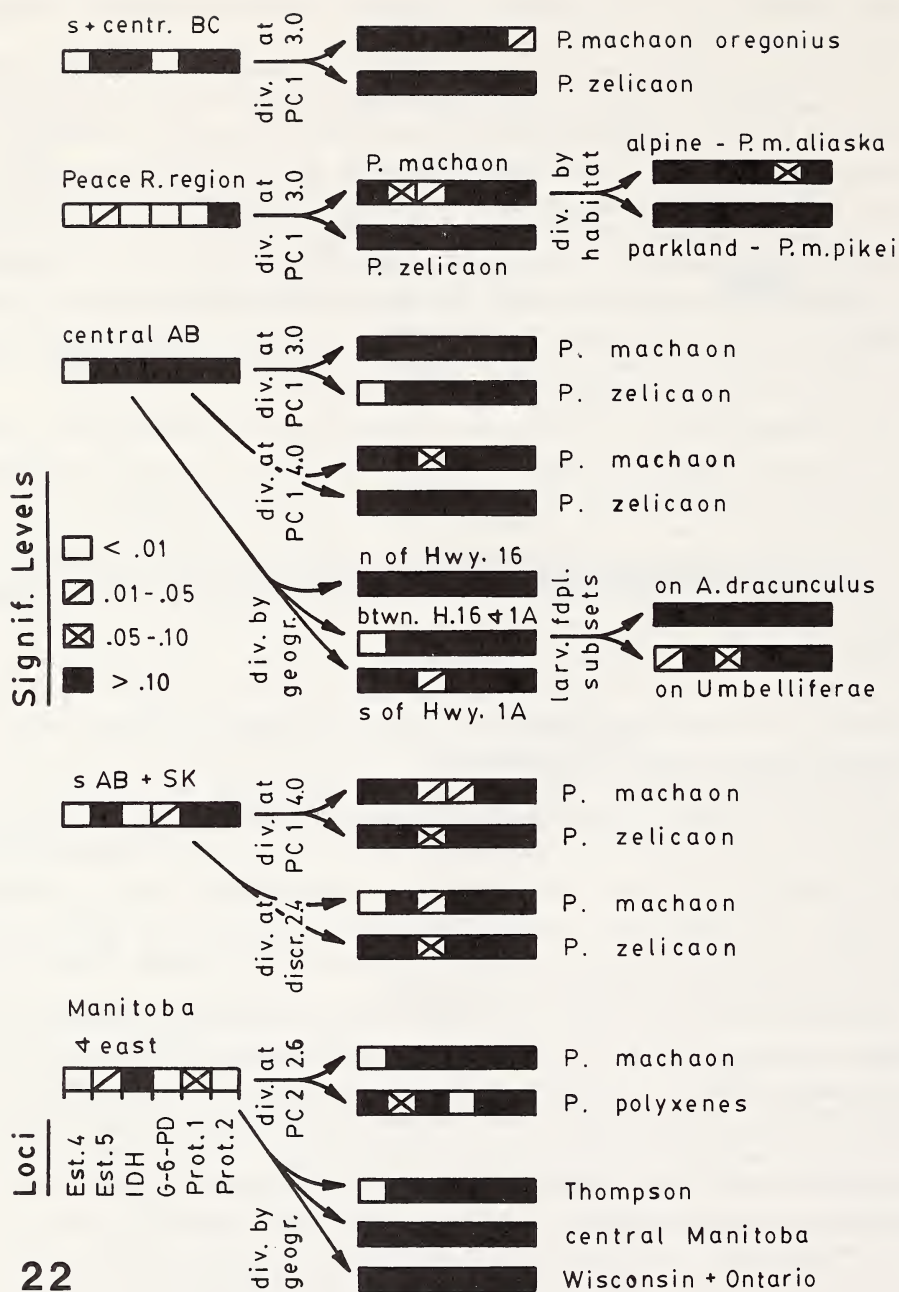
Figure 22. Hardy-Weinberg equilibrium tests on subpopulations. Six loci are shown as squares within bar for each population. Significance levels (key at center left) refer to deviation from equilibrium. Names for some populations refer to population divisions based on artificial criteria, such as arbitrary points on discriminant axes.

wild collected adults from these regions scored on the first discriminant axis (Figures 20–21), a distribution appeared of character combinations similar to that obtained from reared material. This indicated that the reared material probably included a representative sample of the foodplants which larvae of these populations feed on in nature.

Tests for Hardy-Weinberg equilibrium.— Chi-squared tests for deviation from Hardy-Weinberg (HW) proportions of enzyme genotypes were used as an indication of whether or not gene flow occured relatively freely within populations. A sample showing a significant excess of homozygous genotypes at a particular locus then suggests some sort of behavioral or genetic incompatibility between the different alleles. In this study, I assume that homozygous excesses indicate likelihood of positive assortative mating or higher heterozygote mortalities, which in turn suggest the presence of more than one species. I also assume that the different enzyme banding patterns are inherited, and for that reason I refer to "loci" rather than "electrophoretic characters" in this section.

Figure 22 includes all six loci which showed a difference from HW proportions at the 5% level in at least one of the five major geographic regions. Since numerous tests for HW equilibrium were performed, at least some of these are likely to show spurious differences.

HW tests on the six loci showed that all five of the major regions had at least one locus with proportions of genotypes different from equilibrium at the 1% level. This suggested more than one species in each region. However, the pattern of deviation from equilibrium and the loci that deviated were different in each of the region.

In southern and central British Columbia, highly significant excesses were identified of homozygous genotypes at the Est4 and G-6-PD loci. These excesses disappeared when the total regional sample was divided into two groups on the basis of the clusters formed on the first PC axis of the analysis on both electrophoretic and morphometric characters, and the tests were rerun. This corroborates the hypothesis that two species are in that region. The *P. m. oregonius* subsample showed an excess of heterozygotes of the Prot2 locus which was significant at the 3.3 % level. No biological explanation is offered for this.

The total sample from the Peace River region showed large deviations from equilibrium in five of the six loci, due to homozygote excesses. When it was subdivided in the same way as for southern British Columbia, most of these excesses were eliminated in the *P. machaon* and *P. zelicaon* subsamples. A further subdivision of *P. machaon* on the basis of habitat eliminated the slight excesses in the Est5 and IDH loci, and supported the division of *P. machaon* in this region into two ecological races, *P. m. aliaska* and *P. m. pikei*. However, a small homozygote excess showed up in *P. m. aliaska* in the Prot1 locus. The biological significance of this, if any, is unknown, though a reasonably large allele frequency difference at this locus between the two races should be noted.

The central Alberta regional sample was very different from the previous two, despite the fact that the total sample had fairly high frequencies of both of the pairs of alleles at the Est4 and G-6-PD loci which normally distinguish *P. machaon* and *P. zelicaon*. The total sample contained genotypes not much different from equilibrium at any of the loci, except Est4. When *P. machaon* was separated from *P. zelicaon* in the same way as for the Peace River and southern British Columbia regions, the highly significant homozygote excess was retained in the *P. zelicaon* zelicaon subsample. A division of the total sample at 4.0, rather than 3.0, on the same PCA axis showed a slightly significant excess of heterozygotes at the IDH locus. Clearly, the second division furnished subsamples more consistent with the hypothesis that there are two species in that region. However, it divided the total central Alberta sample down the middle of

Table 5. Morphometric character state distributions for population samples of the *P. machaon* species group

Abbreviations: n of H.16 = central Alberta region, north of Highway 16. Hwy. 16-1A = central Alberta region between Highways 16 and 1A. s+c BC = southern and central British Columbia. s AB = southern Alberta. DHW = dorsal hindwing, VFW = ventral forewing.

Character	State	*Papilio machaon* oregonius	pikei	aliaska	hudsonianus	dodi	*Papilio zelicaon X machaon* n of Hwy. H.16	Hwy. 16-1A	Bragg Cr.	*Papilio zelicaon* s+c BC	Peace area	s AB	*Papilio polyxenes asterias*	*Papilio polyxenes X machaon*
N:		55	41	79	37	147	62	90	72	12	50	52	21	10
1. DHW anal yellow	1	5.5	92.7	49.4	94.6	23.1	72.6	72.2	72.2	75.0	74.0	84.6	100.0	90.0
	2	27.3	7.3	34.2	5.4	51.7	24.2	24.4	23.6	16.7	22.0	11.5		10.0
	3	56.4		16.6		25.2	3.2	3.3	4.2	8.3	4.0	3.8		
	4	10.9												
2. DHW pupil shape	1	7.3	87.8	43.0	10.8	2.7	3.2	1.1						80.0
	2	83.6	12.2	51.9	86.6	81.0	14.5	41.1	68.1		2.0		4.8	20.0
	3	9.1		5.1	2.7	14.3	32.3	31.1	27.8	8.3	20.0	5.8	61.9	
	4					2.0	50.0	26.7	4.2	91.7	78.0	94.2	33.3	
3. DHW blue/red sep.	1	36.4	82.9	77.2	32.4	2.7	8.1	7.8	5.6					10.0
	2	32.7	17.1	19.0	29.7	17.7	11.3	25.6	29.2		8.0	1.9		20.0
	3	30.9		3.8	37.8	79.6	80.6	66.7	65.3	100.0	92.0	98.1	100.0	70.0
4. tegula color	1	100.0	100.0	100.0	100.0	99.3	100.0	98.9	98.6	100.0	100.0	100.0		30.0
	2					0.7		1.1	1.4				19.0	40.0
	3												81.0	30.0
5. VFW discal color	1	100.0	92.7	100.0	89.2	10.2	11.3	4.4	11.1		2.0		100.0	10.0
	2		7.3		8.1	22.4	16.1	15.6	11.1		10.0			90.0
	3				2.7	29.3	24.2	33.3	19.4	16.7	28.0	5.8		
	4					38.1	48.4	46.7	58.3	83.3	60.0	94.2		
6. VFW apical smudge	1	100.0	100.0	100.0	100.0	100.0	100.0	96.7	93.1	100.0	100.0	96.2	33.3	20.0
	2							3.3	6.9			3.8	66.7	30.0
	3													50.0

Table 5. continued

		Papilio machaon					Papilio zelicaon X machaon		Papilio zelicaon			Papilio polyxenes asterias	Papilio polyxenes X machaon
Character	State	oregonius	aliaska	pikei	hudsonianus	dodi	n of Hwy H.16 16-1A	Bragg Cr.	s+c BC	Peace area	s AB		
7. VHW postmedian orange	1-2	12.8	34.1	70.9	45.9	5.4	8.0	4.2	8.3	8.0	1.9		10.0
	3-4	80.0	65.9	29.1	54.1	88.2	80.6	72.2	91.7	82.0	80.4		20.0
	5-6	7.2				2.0	9.7	11.1		8.0	7.7	100.0	70.0
	7-8					4.0	1.6	12.5		2.0			
8. metathoracic color	1	100.0	100.0	100.0	100.0	27.2	11.3	20.8	100.0	4.0	82.7	100.0	10.0
	2					71.4	88.7	58.3		96.0	17.3		90.0
	3					1.4		20.8					
9. abd. ventral line	1-3	98.2	100.0	100.0	100.0	21.8	10.0	16.7			1.9		10.0
	4-5	1.8				6.1	4.4	4.2					
	6-7					9.5	2.2	5.6		4.0			
	8-9					62.2	81.1	73.6	100.0	96.0	98.1	100.0	90.0
10. abd. lateral line	1	100.0	100.0	100.0	100.0	98.6	93.3	90.3	100.0	100.0	90.4	100.0	10.0
	2					1.4	1.1	1.4			1.9		90.0
	3						5.6	8.3			7.7		
11. abd. upper line	1-3							4.2					
	4-5				16.2		6.7	9.7			1.9		
	6-7		14.7	2.5	45.9	3.4	13.3	23.6			3.8		3.2
	8-9	100.0	85.3	97.5	37.8	96.6	80.0	62.5	100.0	100.0	94.2	100.0	96.8

Table 6. Allele frequencies, by region, taxon and hybrid assemblage of the *P. machaon* species group.

Abbreviations: see caption for Table 5.

Locus	Allele	RF	*Papilio machaon* oregonius	*P. machaon* aliaska	*P. machaon* pikei	*P. machaon* hudsonianus (Thompson)	*P. machaon* dodi	*P. machaon* X *zelicaon* n of Hwy 16	*P. machaon* X *zelicaon* Hwy 16 to 1A	*P. machaon* X *zelicaon* Bragg Creek	*Papilio zelicaon* cent. + s BC	*P. zelicaon* Peace region	*P. zelicaon* s AB	*Papilio polyxenes asterias* WN + ON	*Papilio polyxenes* X *machaon* cent. MB
αGPD	(n)		57	50	92	39	170	76	102	79	12	61	60	21	10
	A	.29	0.974	1.000	1.000	1.000	1.000	0.993	1.000	0.994	1.000	1.000	0.017	1.000	1.000
	B	.32	0.026					0.007		0.006			0.975		
	C	.35											0.008		
G-6-PD	(n)		55	50	90	39	157	66	96	74	12	61	56	21	10
	E	.16					0.006					0.008			
	A	.18	0.073	0.020	0.128	0.038	0.089	0.136	0.047	0.027		0.016			0.200
	B	.20	0.064	0.010	0.039	0.026	0.092	0.455	0.370	0.385		0.762	0.759		0.050
	I	.22			0.011		0.003	0.030	0.026	0.007		0.016	0.008		0.050
	K	.24			0.006										
	C	.26	0.800	0.970	0.817	0.936	0.739	0.311	0.510	0.554	0.958	0.172	0.214	0.976	0.700
	D	.30	0.064				0.070	0.038	0.042	0.027	0.042	0.025	0.018	0.024	
IDH	(n)		55	50	85	39	154	63	96	74	12	61	56	21	10
	A	.16	0.091			0.026	0.045	0.008	0.057	0.007					
	B	.18	0.664	0.720	0.947	0.679	0.545	0.873	0.724	0.689	1.000	0.984	0.938	1.000	0.900
	C	.20	0.045	0.020		0.026	0.049	0.008	0.026	0.027			0.036		
	D	.22	0.182	0.260	0.053	0.269	0.360	0.111	0.193	0.277		0.016	0.027		0.100
	E	.24	0.018												
MDH	(n)		57	50	93	39	165	70	102	74	12	63	17	21	10
	I	.16									0.042		0.018		
	A	.18		0.030	0.005	0.038	0.006	0.021	0.054	0.047			0.009		
	B	.22	1.000	0.970	0.995	0.962	0.988	0.979	0.946	0.946	0.958	1.000	0.964	0.976	0.950
	C	.26					0.006			0.007			0.009	0.024	0.050
ME	(n)		55	50	91	39	162	71	96	79	12	61	56	21	10
	J	.475	0.009			0.077	0.046	0.021	0.010	0.038	0.083			0.071	0.100
	I	.500	0.164	0.010		0.244	0.185	0.056	0.047	0.051	0.125	0.074	0.027	0.071	0.100
	A	.525	0.291	0.170	0.242	0.641	0.707	0.908	0.901	0.880	0.792	0.893	0.857	0.143	0.750
	B	.550	0.536	0.820	0.758									0.643	
	K	.575					0.006								
	C	.600				0.038	0.052	0.014	0.010	0.032		0.033	0.027	0.048	0.050
	D	.625					0.003		0.031				0.089	0.024	

Table 6. continued

			Papilio machaon					Papilio machaon X zelicaon			Papilio zelicaon			Papilio polyxenes asterias	Papilio polyxenes X machaon
Locus	Allele	RF	oregonius	aliaska	pikei	hudsonianus (Thompson)	dodi	n of Hwy 16	Hwy 16 to 1A	Bragg Creek	cent. + s BC	Peace region	s AB	WN + ON	cent. MB
ODH	(n)		55	48	84	39	156	63	96	74	12	59	56	21	10
	A	.17	0.009	0.021	0.958	0.115	0.006	0.040	0.063	0.162		0.102	0.036		0.050
	B	.21	0.991	0.760	0.042	0.795	0.994	0.857	0.875	0.811	1.000	0.822	0.946	1.000	0.950
	C	.25		0.219		0.090		0.103	0.063	0.027		0.076	0.018		
APK	(n)		55	45	82	39	154	63	96	74	12	53	56	21	10
	A	.55	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.991	1.000	1.000
	B	.60											0.009		
Est4	(n)		59	50	98	39	163	75	102	79	12	61	59	21	10
	A	.48	1.000	0.920	0.954	0.897	0.954	0.293	0.475	0.677	1.000	0.074	0.085	1.000	0.950
	B	.54		0.080	0.046	0.103	0.046	0.707	0.525	0.323		0.925	0.915		0.050
Est5	(n)		59	50	96	39	163	75	102	79	12	61	56	21	10
	I	.57	0.008		0.510	0.077	0.009	0.053	0.108	0.006		0.049	0.071		0.150
	A	.64			0.010	0.013		0.007				0.008			
	B	.65	0.297	0.080			0.337			0.146					0.050
	C	.71	0.695	0.920	0.479	0.910	0.653	0.893	0.873	0.842	0.958	0.902	0.929	0.952	0.800
	D	.75						0.047	0.020	0.006	0.042	0.041		0.048	
Prot1	(n)		55	45	82	39	154	63	96	74	12	52	56	21	10
	A	.21	1.000	0.789	0.598	0.897	0.997	0.722	0.940	0.625	1.000	0.952	1.000	1.000	1.000
	B	.26		0.211	0.402	0.103	0.003	0.278	0.060	0.375		0.048			
Prot2	(n)		55	45	82	39	154	63	96	74	12	52	56	21	10
	I	.300					0.026		0.010			0.019			
	A	.315	0.400	0.022	0.018	0.064	0.224	0.071	0.130	0.007	0.333	0.135	0.455	0.500	
	B	.330	0.600	0.956	0.970	0.038	0.727	0.921	0.844	0.088	0.667	0.837	0.536	0.500	0.976
	C	.345		0.022	0.012	0.897	0.023	0.008	0.016	0.905		0.010	0.009		0.024
Heterozygosity:			0.233	0.155	0.188	0.203	0.218	0.196	0.219	0.246	0.076	0.162	0.158	0.078	0.191

a somewhat bell-shaped curve of character combinations (Figure 12), and may simply reflect the large contribution of the Est4 locus to the scores on that axis.

With division of the sample from central Alberta region into three subregions (a northern, middle and southern one), both the northern and southern subregions appeared not to be significantly different from equilibrium at the Est4 locus either, despite the higher proportion of alleles characteristic of *P. zelicaon* in the northern subregion (Table 6). This was especially interesting in the sample for the southern subregion, since it was composed of specimens from only a single locality at Bragg Creek. The deviation from equilibrium in the Bragg Creek sample at the IDH locus was caused by an excess of heterozygotes. The sample from the middle subregion continued to show an excess of homozygotes at Est4. With specimens reared on different foodplants considered separately, it was clear that a slightly less significant excess remained at that locus. These adults were obtained from larvae collected on *Heracleum* plants (Umbelliferae).

The highly significant homozygote excess was retained even with the largest sample from a single locality in that subregion, Buck Lake, considered separately (not shown on Figure 22). This locality is, to my knowledge, about 80 km from the nearest stand of *Artemisia dracunculus*. These results suggest that *P. machaon* and *P. zelicaon* have merged their gene pools in a large part of the central Alberta region, although not all loci are at equilibrium in the middle part of that region.

The regional sample from southern Alberta and Saskatchewan showed significant homozygote excesses at three loci. A division of the sample on the basis of scores on the first PCA axis of the analysis on both morphometric and electrophoretic characters eliminated the excess at the Est4 locus, but only reduced it at the IDH and G-6-PD loci. With the sample divided on the basis of scores on the first axis of the discriminant analysis of reared specimens, the homozygote excesses were retained at the Est4 and IDH loci. Division of the sample from this region into two species is supported by the fact that the homozygote excesses were partially reduced even when the sample was subdivided on the basis of just morphometric characters.

However, this subdivision is not as good as that effected in the southern British Columbia and Peace River regions. One reason may be a higher probability of incorrect species assignment, because of the greater morphometric similarity between *P. machaon* and *P. zelicaon* from this region. A second explanation is that, even though the species retain a separate genetic identity, there is a biologically significant amount of gene introgression between the species. The rate of introgression may differ between loci, as for example between Est4 and G-6-PD. This suggestion is supported by the fact that these two loci have very similar differences in allele frequency between *P. machaon* and *P. zelicaon* in the southern British Columbia and Peace River regions, and yet G-6-PD seems to have reached equilibrium before Est4 in the middle part of the hybrid zone in central Alberta.

In the region that included samples from Manitoba, Wisconsin and Ontario, there was also evidence for two species, with some hybridization between them. Here the main alleles distinguishing between *P. polyxenes* and *P. machaon* were G-6-PD and Prot2, rather than G-6-PD and Est4, as between *P. zelicaon* and *P. machaon*. The total regional sample had several significant deviations from equilibrium. When it was divided on the basis of scores on the second PCA axis using both morphometric and electrophoretic characters, which essentially separated black morph from yellow morph individuals, then a highly significant deviation remained at the G-6-PD locus in the sample comprised of black morph specimens. These deviations were eliminated when the region was divided geographically into three subregions.

The main difference from the previous subdivision was that one yellow morph and nine black morph specimens were placed in a group by themselves. Under both schemes there was a significant excess of homozygotes in the Est4 locus of the northern Manitoba sample, because of presence at Thompson of two individuals homozygous for the "B" allele (most common in *P. zelicaon*), compared with only four heterozygous individuals and 33 individuals homozygous for the "A" allele (most common in *P. machaon* and *P. polyxenes*). I can offer no convincing biological explanation for this situation, since Thompson is many hundreds of kilometers from the nearest localities where *P. zelicaon* specimens have been found. Instead, I suspect, it may be due to sampling error. Clearly, more work is needed to ascertain species relationships in Manitoba.

Diagnosis of Adults and Ranking of Taxa

To tabulate character variation quantitatively, 13 major populations were defined. The arrangement of these groups was based on both electrophoretic and morphometric characters, and the groups resemble those described in the previous sections involving multivariate analyses and Hardy-Weinberg equilibria. Table 6, for electrophoretic characters, includes some specimens for which not all loci were scored, but for which it was possible to be certain of their identification by reference to their morphometric characters. Table 5, for morphometric characters, includes data only for those specimens used in the PCAs.

Papilio machaon.— In general, *P. machaon* adults from western Canada were distinguished by yellow hair on the ventral part of the thorax and abdomen, yellow scales covering most of the forewing disc on the ventral side, and the anal pupil connected to the wing margin, whether club shaped or a thin line. This result verifies the utility of the color pattern characters of adults used by others to identify this species (*e.g.,* Edwards, 1883; Dornfeld, 1980). In electrophoretic characters, *P. machaon* individuals were distinguished by the A allele at Est4, the C allele at G-6-PD and a relatively high proportion of D alleles at IDH.

P. m. dodi specimens were more difficult to identify in the absence of electrophoretic information, but could best be distinguished from the *P. zelicaon* populations sympatric with them by the club shaped, connected anal pupil. I have examined the types of *P. m. dodi* in the Canadian National Collection, and they definitely belong to the race of *P. machaon* whose larvae feed on *Artemisia dracunculus* on the prairies of southern Alberta and Saskatchewan.

Subspecies of *P. machaon* in western Canada were best separated from each other by locality and habitat, though there were major changes in the frequency of particular states of several characters, including IDH, ODH, Est4, Prot1 and Prot2. Though almost all specimens of *P. m. oregonius* and *P. m. dodi* from western Canada are distinguished by both adult and larval color pattern, these two subspecies grade into each other in western Montana and southern Idaho. Since the zone of intergradation is narrow, relative to the phenetically more homogeneous ranges of the subspecies, I recognize the populations on either side of the continental divide in Montana and northward as separate subspecies.

I am uncertain of the extent and location of the intergradation between these subspecies south of Montana. In Utah and Colorado, the black adult wing morph becomes more common (Emmel, 1975) and the name *P. machaon bairdii* should be applied. The name *P. brucei* has been applied to yellow morph adults in polymorphic populations within the range of *P. m. bairdii*(Figure 42). Its type locality is from the northern part of the major clinal shift to yellow forms, and its use in a subspecific sense is probably not of much value. I follow the practice of Fisher (1980) and Miller and Brown (1981) in treating the name as a junior synonym of *P. m.*

bairdii,

The previous subdivision of the southern subspecies of *P. machaon* as separate species is probably a consequence of W.H. Edwards' relatively typological species concept, and the natural tendency of many workers to view the black morph adults as fundamentally different from the yellow morph adults. However, black morph adults of *P. machaon* occur in low frequencies as far north as Drumheller, Alberta, where they are electrophoretically identical to the yellow morph adults. Hence, I feel that the inclusion of *P. bairdii* in *P. machaon* is an inescapable consequence of the application of the biological species concept to geographic clines. Fisher (1980) has also recognised the specific unity of all the *Artemisia dracunculus*-feeding populations in the western United States.

Papilio zelicaon and hybrids.— Most *P. zelicaon* individuals from western Canada are recognized by the black hair on the ventral part of the thorax and abdomen, black or almost black ventral forewing disc and the rounded, centered anal pupil. As in *P. machaon*, these characters match those previously used in traditional taxonomic treatments. Important diagnostic electrophoretic characters included the B allele in both the Est4 and G-6-PD loci.

I do not believe that formal subspecific divisions are justified in *P. zelicaon*. The species is composed of innumerable slightly differentiated populations with adult features that grade into each other. Local foodplant and climatic adaptations of most populations are usually far more pronounced than are the relatively minor differences in morphometric characteristics. I believe that the recent practice, of referring to the populations that Remington (1968a) named *P. gothica* as *P. zelicaon nitra*, is unwarranted. Yellow morph adults are more common than the black form even at the type locality of *P. nitra*, and I find the eastern and western yellow morphs of *P. zelicaon* to be impossible to separate with any degree of consistency.

The presumed type of *P. zelicaon* Lucas was examined for me in considerable detail by G.E. Ball in 1980, on a trip he made to the Paris Museum. Using Ball's description and comparative material, as well as photographs of the specimen (taken by J.J. Menier), features of *P. zelicaon* were checked against Remington's (1968a) diagnosis of *P. gothica*. The specimen is closer to Remington's conception of *P. gothica* than his conception of *P. zelicaon*. This is not surprising, since as Shapiro (1975) and Emmel and Shields (1980) pointed out, *P. zelicaon* from the type locality in central California has undergone basic ecological changes since its description in 1852, while the remaining populations at higher altitudes in central California are still very similar in appearance to topotypic *P. gothica.*

In some regions, particularly central Alberta, a high proportion of individuals exhibited intermediate character states, or character combinations which placed them in an intermediate position between *P. zelicaon* and *P. machaon*. These were considered to be hybrids (individuals of mixed ancestry), and such individuals formed the majority of some populations. Since these populations included individuals with phenotypes occupying the complete range between the typical parental forms, many individuals were difficult to identify as hybrids. Hybrid populations were also highly variable in composition, and were only identified as such when they showed a unimodal distribution of phenotypes, of which the peak was clearly intermediate between the parental species.

The *P. zelicaon X machaon* hybrid swarms in the Cypress Hills have been much less completely documented than those in central Alberta. I designate these populations as hybrid swarms mainly because most individuals look very similar to the hybrid material collected in the southern part of central Alberta. As well, they are intermediate in wing and body pattern between the *P. machaon* and *P. zelicaon* specimens collected in the prairie habitats surrounding

the Cypress Hills.

In regions where hybridization between *P. zelicaon* and *P. machaon* is rare, possibly there are structural isolating mechanisms between the species, in addition to behavioral ones. This was suggested by the only natural interspecific mating which I have observed in such regions of sympatry. The mating took place at Taylor, at a site where *P. m. pikei* adults are common, and involved a fresh *P. zelicaon* female and slightly worn *P. machaon* male. They remained in copula for at least 11 hours before they separated. Such an abnormally long mating (Clarke and , 1956b) may result from disturbance of being netted, but seems more likely to be due to some sort of prezygotic mating disfunction.

Papilio polyxenes and hybrids.— Most specimens of *P. polyxenes* were easily distinguished from those of *P. zelicaon*, *P. machaon* and their hybrids by the much greater amount of black scales on the hindwing, covering more than half of the hindwing disc, and yellow spots rather than a broad yellow band on the sides of the abdomen. Separation was also based on the K allele of G-6-PD and the A allele of Prot2.

A small proportion of *P. polyxenes*-like individuals were noted in *P. zelicaon*, *P. machaon* and their hybrids in western Canada. These, however, had the same electrophoretic alleles as the yellow morph individuals with which they were found, and were also distinguished from *P. polyxenes* by the greater amount of yellow on the tegula and apex of the forewing, as well as the lesser amount of orange on the postmedian band of the ventral hindwing. The black morph specimens of *P. zelicaon* from Alberta prairies were identical in appearance to a series which I have seen from the type locality of *P. nitra* in Montana, and so there is no reason to expect these individuals to comprise a separate species outside of western Canada.

Although the morphometric differences between *P. zelicaon* and *P. polyxenes* in western Canada suggest a greater ease of species identification than Fisher (1980) reported in Colorado, I expect that I would have found similar difficulties if I had been able to obtain a larger sample from localities where these two species are in closer contact in southern Saskatchewan.

Since the interactions of *P. polyxenes* with *P. machaon* and *P. zelicaon* in western Canada are not well understood, I rely on the opinions of authors who are familiar with the three species in the western United States (*e.g.,* Ferris and Emmel, 1982; Fisher, 1977 and 1980), and who have consistently reported that *P. polyxenes* maintains a distinct genetic identity from both *P. zelicaon* and *P. machaon* throughout most of their region of potential interaction. As well, although electrophoretic characters indicate some intermediacy in central Manitoba, samples of *P. polyxenes* from Ontario and Wisconsin are as different from *P. zelicaon* and *P. machaon* as these two species are from each other.

Most of the specimens of *P. polyxenes* from southern Manitoba are indistinguishable in appearance from *P. p. asterius* from Ontario and the eastern United States. The remainder show signs of introgression with *P. machaon*. Specimens exhibiting substantial introgression are designated as *P. polyxenes X machaon* hybrids. The identification of such natural hybrid specimens is supported by comparisons with those obtained by artificial hybridization. In particular, many of the adults collected in central Manitoba appear very similar or identical to the hybrids obtained by other workers (see particularly Clarke and , 1953, 1955a; Ae, 1961, 1964; Remington, 1958, 1968a). The same applies to hybrid specimens of *P. zelicaon* and *P. machaon* from central Alberta. These studies clearly indicate the genetic basis of these characters, and for this reason I have used several of these characters in the morphometric portion of this study. I consider the similarity between the experimentally produced and

wild-collected specimens to be adequate evidence for the hybrid origin of the collected material.

Two taxonomic descriptions refer to adult forms which are due to hybridization between *P. polyxenes* and *P. machaon*. These are *P. kahli* and *P. m. avinoffi*, both of which are referred to in this study either as black or yellow wing morph adults of *P. polyxenes X machaon*, or as *P. polyxenes X machaon* and *P. machaon X polyxenes*, respectively. My use of these names is based on photographs I have seen of the holotypes. I have also seen several paratypes, but these differ slightly from one another, as well as from the holotype. At least one of the female paratypes of *P. kahli* in the Canadian National Collection seems to me to be identical to typical *P. p. asterius* specimens. My opinion was apparently shared by J.D. McDunnough, who indicated his opinion on a folded slip of paper attached to the specimen pin.

Specimens which fit the description of *P. m. avinoffi* were obtained by Remington (1958, 1968a), when he crossed two comparatively yellowish individuals of the black adult morph from central Manitoba, and got some yellow morph as well as black morph offspring. The *avinoffi* form tends to grade into more typical *P. m. hudsonianus* and so identification of specimens is arbitrary.

The systematic relationship of *P. polyxenes* and *P. machaon* in central Manitoba clearly needs more investigation than I have provided in the present study. The recognition of central Manitoba populations as interspecific hybrid populations, rather than as intermediates between subspecies, allows the retention of established taxonomic practice, pending a more thorough study of these two taxa in this region, as well as elsewhere in their ranges.

Ranking and accuracy of identification.— The distribution of morphometric and electrophoretic character states showed, in several ways, that more than one species of the *P. machaon* group was present in western Canada. First, multivariate analysis of either of these two character suites indicated three major clusters of individuals in western Canada, and two major clusters in each of four of the five regions in western Canada. Second, the proportions of enzyme genotypes suggested interruptions to gene flow which corresponded to the breaks between clusters in most of western Canada. Third, the morphometric and electrophoretic character distributions showed good correspondence with each other, as well as with ecological features such as preferred habitat and larval foodplant. This character concordance applied to areas where there appeared to be a large amount of interspecific hybridization, as well as those in which species appeared to interbreed very little. The characters of wing and body color pattern, which had been used by taxonomists in the past to distinguish among species, proved useful under critical examination. A few electrophoretic loci were also diagnostic for species, and so gave additional information about inter- and intra-population relationships.

However, evidence of hybridization between each of the three species showed that recognition of some populations as species, and others as interspecific hybrid swarms or subspecies, was partially arbitrary. This was resolved by an arrangement reflecting the fact that species hybridize only rarely over most of their sympatric range, and that also involved a minimum of change in existing taxonomic arrangements. Since previous taxonomic arrangements were not based on electrophoretic characters, consideration of these allowed an independent test of the biological significance of these arrangements.

The electrophoretic characters also allowed a more direct comparison with the degree of genetic similarity between species of other, unrelated, taxa. This comparison was obtained by calculating Nei's (1972) Genetic Identity (I) for all combinations of each of the 13 geographically separated populations of the *P. machaon* group which showed little or no internal interruption in gene flow. Nei's Genetic Identity is the most commonly used of several

Table 7. Nei (1972) Genetic Identity and Distance for taxa and hybrid assemblages of the *P. machaon* species group.

Mean Genetic Identity is below diagonal and mean Genetic Distance is above diagonal.

Population	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1. *P.m. oregonius*	*****	0.043	0.053	0.029	0.010	0.124	0.072	0.054	0.226	0.196	0.179	0.017	0.145
2. *P.m. aliaska*	0.958	*****	0.038	0.006	0.032	0.094	0.052	0.032	0.234	0.170	0.192	0.047	0.233
3. *P.m. pikei*	0.948	0.963	*****	0.045	0.046	0.123	0.086	0.063	0.258	0.195	0.219	0.062	0.249
4. *P.m. hudsonianus*	0.972	0.994	0.956	*****	0.022	0.191	0.049	0.029	0.221	0.165	0.181	0.038	0.217
5. *P.m. dodi*	0.990	0.969	0.955	0.978	*****	0.102	0.053	0.034	0.217	0.176	0.172	0.027	0.177
6. *P.m.X z.*:n of H.16	0.884	0.911	0.884	0.913	0.903	*****	0.010	0.028	0.039	0.014	0.031	0.097	0.232
7. *P.m.X z.*:Hwy 1A-16	0.930	0.949	0.918	0.953	0.949	0.990	*****	0.007	0.069	0.039	0.048	0.058	0.202
8. *P.m.X z.*:Bragg Cr.	0.947	0.968	0.939	0.971	0.967	0.972	0.993	*****	0.108	0.069	0.083	0.048	0.204
9. *P.zelicaon* : s. BC	0.797	0.791	0.773	0.802	0.805	0.962	0.933	0.898	*****	0.011	0.008	0.188	0.267
10. *P.zelicaon* : Peace	0.822	0.843	0.823	0.848	0.838	0.986	0.961	0.933	0.989	*****	0.013	0.161	0.276
11. *P.zelicaon* : s. AB	0.836	0.826	0.803	0.835	0.842	0.970	0.953	0.920	0.992	0.987	*****	0.140	0.219
12. *P.m. X p.*: c. MB	0.984	0.954	0.940	0.962	0.974	0.908	0.943	0.953	0.829	0.851	0.870	*****	0.109
13. *P. polyxenes*	0.865	0.792	0.780	0.805	0.838	0.793	0.817	0.815	0.766	0.758	0.803	0.897	*****

standardized genetic similarity coefficients, and *I* has been determined for a wide variety of taxa.

Of the 13 major populations distinguished in this study, all pairs listed as separate species had *I* values less than or close to 0.85 (Table 7). These pairs included those populations from the three regions in which *P. machaon* and *P. zelicaon* occur sympatrically. Thorpe (1982) showed that when two populations have an *I* value of less than 0.85, the probability is very high that they are distinct species. Thus, despite difficulties in separating individuals of some populations on the basis of morphometric characters, as well as the presence of several hybrid swarms, genetic similarity coefficients based on elctrophoretic characters suggest that at least the main clusters were different enough to rank as separate species.

I values can also be used to make intraspecific pairwise comparisons. About 80% of conspecific I values are above 0.95 (Thorpe, 1982). In the present study, all comparisons of populations within *P. machaon* and *P. zelicaon* were close to or above 0.95.

The interval between 0.85 and 0.95 is occupied by a few values from interspecific pairs and a much larger proportion of intraspecific pairs. In the *P. machaon* group, those comparisons involving hybrid swarms and one of the parental species generally show *I* values between 0.85 and 0.95. Several of these, however, resemble one parental species more than the other and show *I* values above 0.95 when compared with the more similar species. For example, the northern part of the *P. machaon X zelicaon* swarm is closer to *P. zelicaon* while the southern part (Bragg Creek) is more similar to *P. machaon*. This result could have been expected on the basis of morphometric character similarities. However, the central Manitoba population is much more like *P. machaon* than *P. polyxenes*, a result in contrast to that which might be expected on the basis of morphometric similarities (for rough comparisons see 3D.PCA scores in Figures 7–9).

Without information about locality, habitat or electrophoretic alleles, I estimate that I am able to correctly identify 95% of all specimens from western Canada as members of one of the groups listed in the key in the previous chapter. My accuracy is probably higher for distinguishing *P. machaon* from *P. zelicaon* in the absence of a large hybrid swarm. *P. zelicaon X machaon* and *P. polyxenes X machaon* hybrids, as well as *P. m. dodi*, are more difficult to distinguish from each other and I estimate that I can correctly identify about three quarters of all such specimens with only morphometric information.

Diagnosis of specimens on the basis of morphometric characters in the key was found to be fairly reliable when compared to scores obtained from PCA factor loadings. Several characters used in the keys were not used in the original multivariate character analyses, generally because they were difficult to score consistently. Both the key and PCA factors produce arbitrary divisions which are not particularly meaningful in hybrid populations.

Since the five subspecies of *P. machaon* are allopatric, or parapatric and separated by habitat in western Canada (see next section), it is possible to obtain a more precise estimate of accuracy of identification. Using habitat and geographic range to define groups, I performed a discriminant function analysis on the five subspecies, using the morphometric and electrophoretic characters which were employed in the multivariate analyses in previous sections. Since sample sizes were small, only the 27 variables which showed more than 10% variation in frequency between groups were used. The results are contained in Table 8.

This analysis indicates that a high frequency of correct identification can be achieved for these taxa if both major character suites are used. The lowest accuracy, 76% for *P. m. hudsonianus*, is still fairly high. If only the 11 morphometric characters listed in Table 2 are

Table 8. Frequency of correct identification of subspecies of *Papilio machaon.*

Values based on discriminant function analysis (DFA) of 27 morphometric and electrophoretic characters. Classification percent shows frequency of correct identification (*e.g.,* 82.9% for *P. m. aliaska*) and incorrect identification (*e.g.,* 9.8 and 7.2 % of *P. m. aliaska* were misclassified as *P. m. hudsonianus* and *P. m. pikei*, respectively).

	Defined Groups	N	1.	2.	3.	4.	5.
					% Classification with DFA		
1.	*P. m. aliaska*	41	82.9	9.8	7.3		
2.	*P. m. hudsonianus*	37	16.2	75.7	8.1		
3.	*P. m. pikei*	79	7.6	1.3	88.6	2.5	
4.	*P. m. oregonius*	55	1.8		1.8	96.4	
5.	*P. m. dodi*	147			1.4	7.5	91.2

used in a new DFA, rather than the 27 morphometric and electrophoretic characters used to obtain the results in Table 9, then the lowest accuracy is 62%, again for *P. m. hudsonianus.* However, if forewing length and tail length are added to these 11 characters, and a third DFA is performed, then the accuracy of correct identification of *P. m. hudsonianus* rises to 70%, and the lowest is 68%, for *P. m. pikei*. I estimate that my personal lowest accuracy of identification of these five *P. machaon* subspecies is 75% if characters such as wing shape and color are considered, which are difficult to quantify for computer work.

It is difficult to obtain a precise assessment of the relative systematic utility of morphometric and electrophoretic characters in the context of the present study. The morphometric characters were chosen on the basis of their variability within western Canada, and also as a means of comparison to systematic descriptions and diagnoses. Electrophoretic characters were selected much more randomly, since any protein that showed consistent, simple banding patterns was used. As well, only three loci showed more than 50% allele frequency differences between populations, and it is possible that results were affected by sampling error. Furthermore, the coding scheme for morphometric characters was somewhat different from that used for electrophoretic characters in the principal components analyses. A more strictly analogous scheme would have reduced the number of electrophoretic characters from 42 to 10, a number more comparable to the 11 morphometric characters used. Despite these factors, it is clear that electrophoretic analysis is of considerable systematic utility (*cf* Wake, 1981). The large degree of correspondence of the two types of characters in the context of the present study is a demonstration of the potential usefulness of electrophoretic analysis in systematic research on species complexes.

Larval Color Pattern

Larvae of *P. machaon, P. zelicaon* and *P. polyxenes* do not show consistent interspecific differences in color pattern, though intraspecific variability is marked. Most fifth instar larvae of these three species are predominantly green, with a prominent black band extending around each segment, and six colored spots on most segments. Within populations, the background green color varies from pale bluish-green to bright emerald green, and the black bands vary considerably in width. Color of the segmental spots varies from lemon yellow to orange-red.
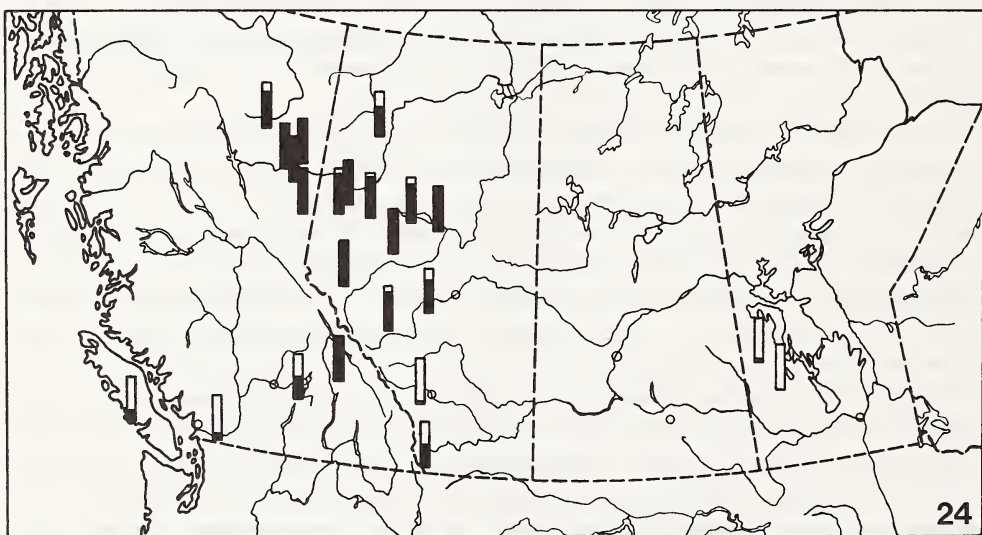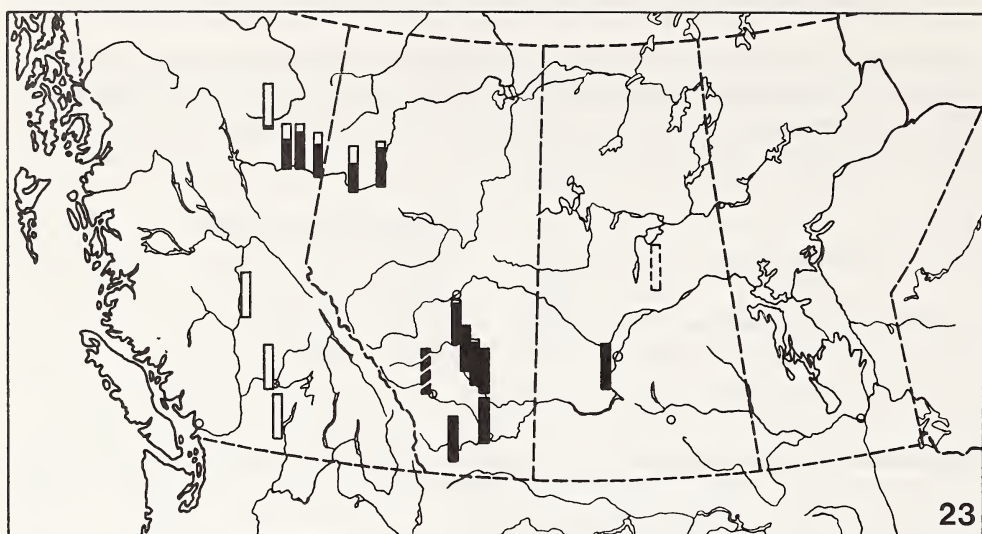
Figures 23 and 24. Frequencies of spot color in larvae of the *P. machaon* group in western Canada. Dark areas of histograms indicate orange or red spots, and light areas indicate yellow spots. Figure 23. Spot colors of larvae collected on composites. Histograms with broken borders indicate small sample sizes. Figure 24. Spot colors of larvae collected on umbellifers.

Griffiths, G.C.D. (1986, 22: 253–260).–Relative Abundance of the Root Maggots *Delia radicum* (L.) and *D. floralis* (Fallén) (Diptera: Anthomyiidae) as Pests of Canola in Alberta.

page

256

Fig. 2

Substitute following figure for the one on page 256.
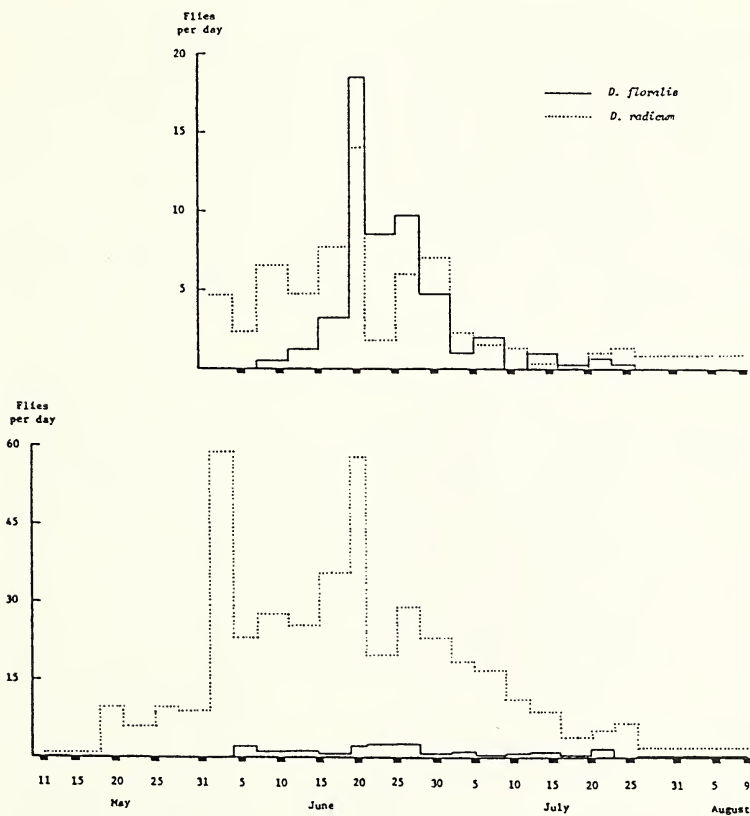
The larvae of *P. alexanor* have a color pattern which is very similar to that of the above three species, despite a very different adult wing pattern. *P. indra* and *P. hospiton* each have a larval color pattern which is divergent from that of the other species in the *P. machaon* group, but which is more similar to that of other *P. machaon* group members than to other *Papilio*.

Color of the segmental spots on mature larvae is consistent on individuals, but many larval populations are composed of discrete color classes with few intermediates. Clarke and Knudsen (1953) were the first to study the genetic mechanism controlling spot color, by crossing yellow-spotted *P. polyxenes* larvae with orange-spotted *P. machaon* larvae, to produce orange-spotted hybrids. Clarke and Sheppard (1955b, 1956a) later showed that the hybrid larvae had spots which were a paler orange than those of *P. machaon*, and although yellow is recessive to orange, the degree of dominance of the orange allelomorph varies with the subspecies of *P. machaon*, They suggested that inheritance was controlled by more than one allele which could produce orange spots, or through modifiers at another locus. Clarke *et al.* (1977) established that the main locus controlling larval spot color was not linked to the locus controlling black and yellow wing morphs in adults.

P. machaon, *P. zelicaon*, *P. polyxenes* and *P. indra* are to some extent all polymorphic for larval spot color. Thus, this polymorphism probably predates the most recent common ancestor of these species. Nonetheless, differences in spot color have been used to support some taxonomic distinctions. For example, Remington (1968a) considered the fact that he had found and reared only yellow-spotted larvae of *P. gothica* as evidence contributing to his decision to name it as a separate species. His sample was comprised of few independent observations and provided little support for his decision, considering that most populations of *P. zelicaon* were known to produce both yellow and orange spotted larvae (Clarke and Sheppard, 1970). All 34 late-instar larvae which I found at Gothic had yellow spots, supporting Remington's observation of apparent allelic homogeneity at that locality. It would be interesting to determine if larvae of *P. zelicaon* in central Colorado generally have yellow spots and if their proportion decreases in populations farther away from *P. polyxenes*.

In western Canada, many samples from single localities contained a mixture of both yellow-spotted and orange-spotted larvae, but there were also a number of interesting frequency shifts between different taxa and between different regions (Figures 23–24).

The largest differences in frequency of spot color occurred within *P. machaon*. All larvae collected on *Artemisia dracunculus* in southern and central British Columbia had yellow spots, while in southern Alberta and Saskatchewan 99.6% had orange spots. Thus *P. m. dodi* and *P. m. oregonius* may have undergone a complete allele substitution over much of their range in western Canada. I do not know what the predominant spot color is where these races contact each other in the western United States.

In the Peace River region 28% of the larvae of *P. m. pikei* had yellow spots. If spot color is controlled by a single gene with orange dominant over yellow, then the Peace River *A. dracunculus*-feeding populations have a 50:50 ratio of these two alleles, making them exactly intermediate between *P. m. dodi* and *P. m. oregonius*.

There were far more yellow-spotted larvae in *P. m. aliaska* than in *P. m. pikei*, since 95% of the larvae collected on *A. arctica* had yellow spots. The single larva of *P. m. hudsonianus* which was scored (from a photograph by G. Anweiler) also had yellow spots. Thus *P. machaon* is clearly polymorphic for spot color in North America, but different ecological and geographic races have major frequency differences in spot color.

Samples of larvae collected on umbellifers in almost all localities from Alberta and British Columbia were polymorphic for spot color. Hence geographically separate populations of *P. zelicaon* and its hybrids may have quite different frequencies of spot color, as in *P. machaon*. However, the frequency shifts seem to be somewhat more clinal. Also, *P. zelicaon* larvae consistently had different spot color frequencies from *P. machaon* where these species have low hybridization rates. In Interior British Columbia and the Peace River region, *P. zelicaon* larvae had more orange spots, while in southern Alberta they had more yellow spots.

Hybrid populations did not show much difference from parent species. In central Manitoba, most of the larvae had yellow spots, while *P. polyxenes* larvae generally have yellow spots farther to the southeast, and the only known larval *P. m. hudsonianus* also had yellow spots. In central Alberta the northern populations have mostly orange spots and in this respect merge into the *P. zelicaon* populations farther to the north and west. This trend is mirrored in the adult morphometric and electrophoretic characters of these populations.

The shift toward predominantly yellow spots in the *P. zelicaon X machaon* hybrid swarm west of Calgary is more abrupt. Also, it is interesting to note that the only larva found on *Heracleum* at Bragg Creek had orange spots, while 42 of 44 on *Zizia* had yellow spots. *Heracleum* is a much more common foodplant for *P. zelicaon* populations immediately to the west, and larvae of these populations may have developed from eggs laid by a typical *P. zelicaon* that strayed in from the west. The fact that *P. m. dodi* larvae almost always have orange spots, even at the outer edges of the range of this subspecies, distinguishes the latter from the southern hybrid populations. This supports the contention that hybrid populations are the result of hybridization of *P. zelicaon* with races similar to *P. m. hudsonianus*, rather than to *P. m. dodi*.

ECOLOGICAL CHARACTERISTICS

Geographic Distribution and Habitat

The *Papilio machaon* group has a generally Holarctic distribution. Of the eight species recognized, four are restricted to North America, *P. alexanor* and *P. hospiton* occur only in western Eurasia, and *P. machaon* spans both continents. *P. polyxenes* is found mainly in North America, but is the only species that also occurs in South America.

Species of the *P. machaon* group which have broad ranges also show a considerable diversity of habitat use. For example, different populations of *P. machaon* occur in habitats varying from cool temperate wetlands (Wiklund, 1974; Dempster and Hall, 1980) to hot Saharan deserts (Larsen, 1980), and in Nepal two distinct races are separated only by a continuous cloud belt (Dierl, 1976). Such varied habitat use may occur with relatively little evidence of regional morphological differentiation, as in mountain- versus prairie-adapted populations of *P. zelicaon*.

The three species of the *P. machaon* group living in western Canada interact in a complex pattern of geographic overlap, replacement along contact zones, and varying frequencies of hybridization (Table 9). *P. machaon* has five subspecies in this area, and is the only species which is represented by more than one subspecies. The subspecies of *P. machaon* are all either allopatric with each other, or parapatric but with very limited opportunities for gene flow (Figures 25 and 26). *P. m. hudsonianus* is rare in northern Alberta and northwestern Saskatchewan (*e.g.,* Bird *et al.*, 1982), and there is little opportunity for contact with either *P. m. aliaska* or *P. m. pikei*. *P. m. dodi* and *P. m. oregonius* are separated from the northern subspecies and, in Canada, from each other.

Table 9. Geographic contact between taxa and hybrids of the *P. machaon* group and frequency of black morphs in western Canada.

S = sympatry, with habitat segregation
P1 = abrupt geographic replacement, with low frequency of hybrids
P2 = separated by zone of low population density
P3 = clinal merging of populations
A = allopatry, with disjunction of more than 100 km

	Taxa and Hybrids	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	Black Morph
1.	*P. m. aliaska*												0
2.	*P. m. hudsonianus*	P2											0
3.	*P. m. pikei*	P1	P2										0
4.	*P. m. oregonius*	A	A	A									0
5.	*P. m. dodi*	A	A	A	A (P3 in western U.S.)								2%
6.	*P. zelicaon* X *machaon* -central Alberta	A	P2	A	A	P1							0 (north) to 12% (south)
7.	*P. zelicaon* X *machaon* -Cypress Hills	A	A	A	A	P1	A						approx. 12%
8.	*P. zelicaon* -southern British Columbia	A	A	A	S	A	P1	A					0
9.	*P. zelicaon* -Peace River region	P1	P2	S	A	A	P3	A	P3				0
10.	*P. zelicaon* -southern Alberta & Sask.	A	A	A	A	S	P1	P3	P3	P2			5-15%
11.	*P. polyxenes* X *machaon* -central Manitoba	A	S	A	A	A	A	A	A	A	P2		approx. 97%
12.	*P. p. asterius*	A	P1	A	P2	P2	A	A	A	A	P2	P3	100%
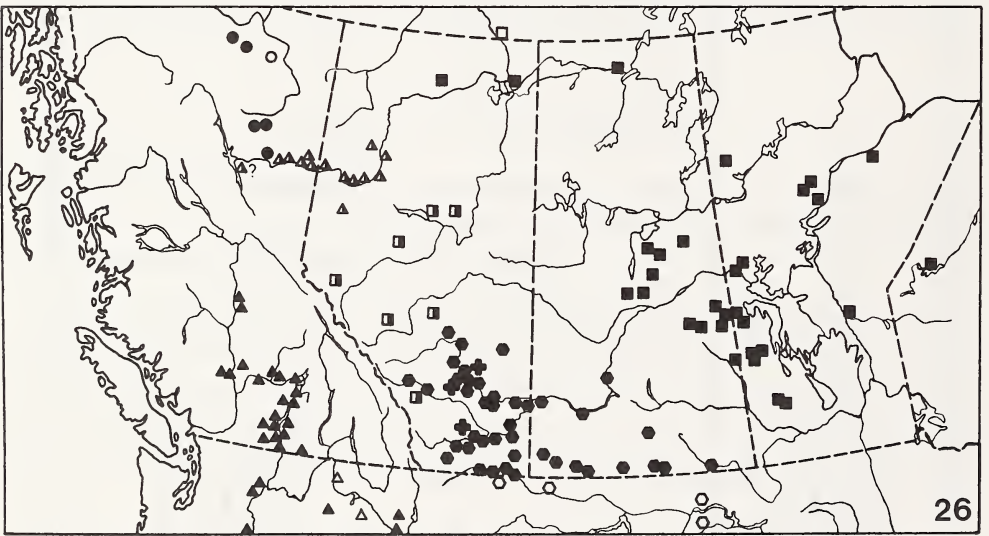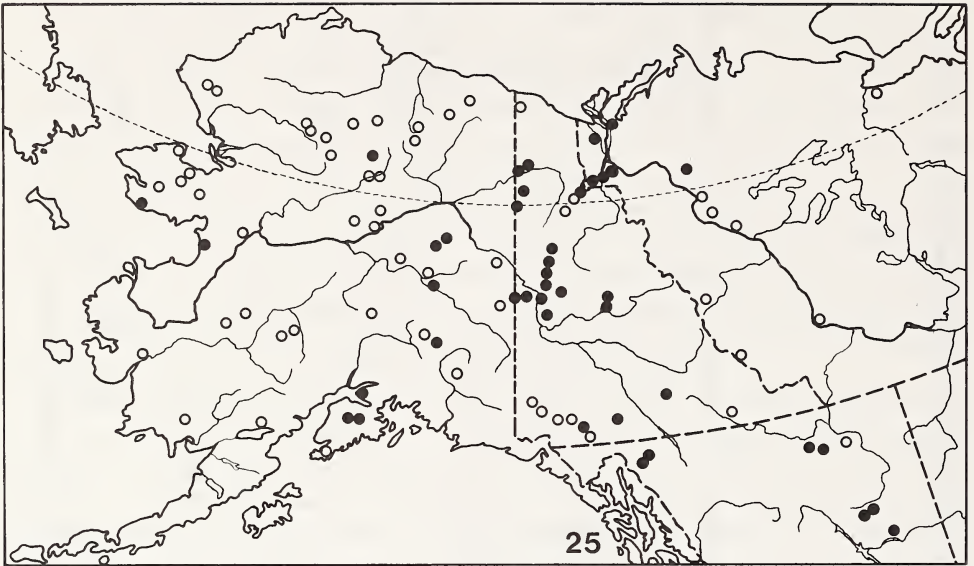
Figures 25 and 26. Empty symbols indicate unverified published records. Figure 25. Distribution of *P. m. aliaska*. Figure 26. Distribution of *P. machaon* in western Canada.
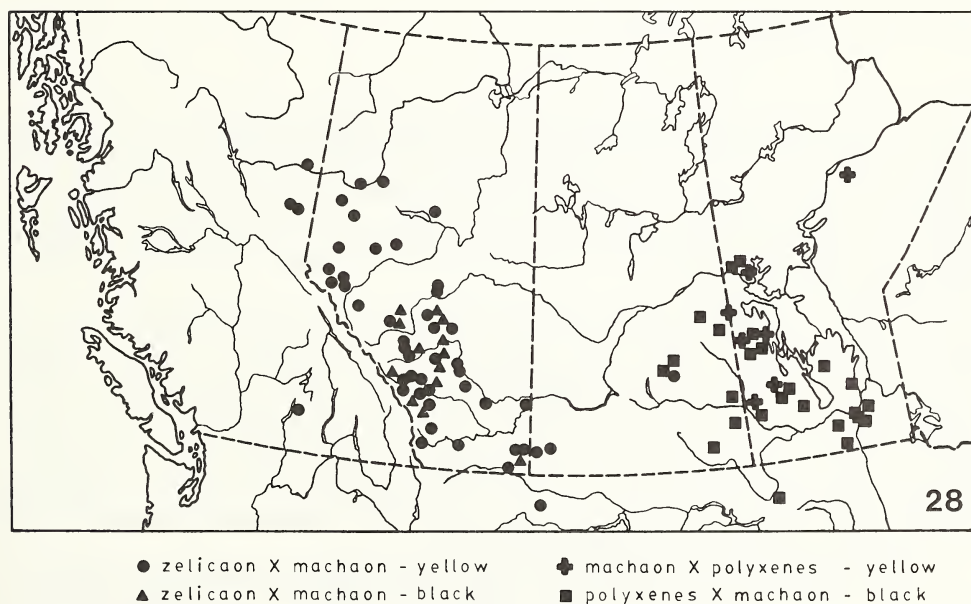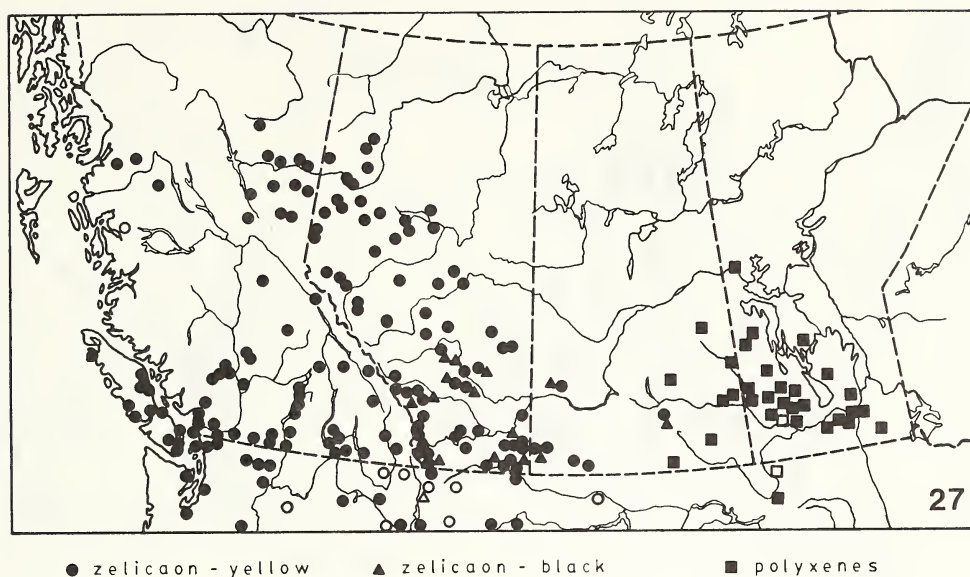
Figures 27 and 28. Figure 27. Distribution of *P. zelicaon* and *P. polyxenes asterius* in western Canada. Empty symbols indicate unverified published records. Figure 28. Distribution of interspecific hybrids in western Canada.
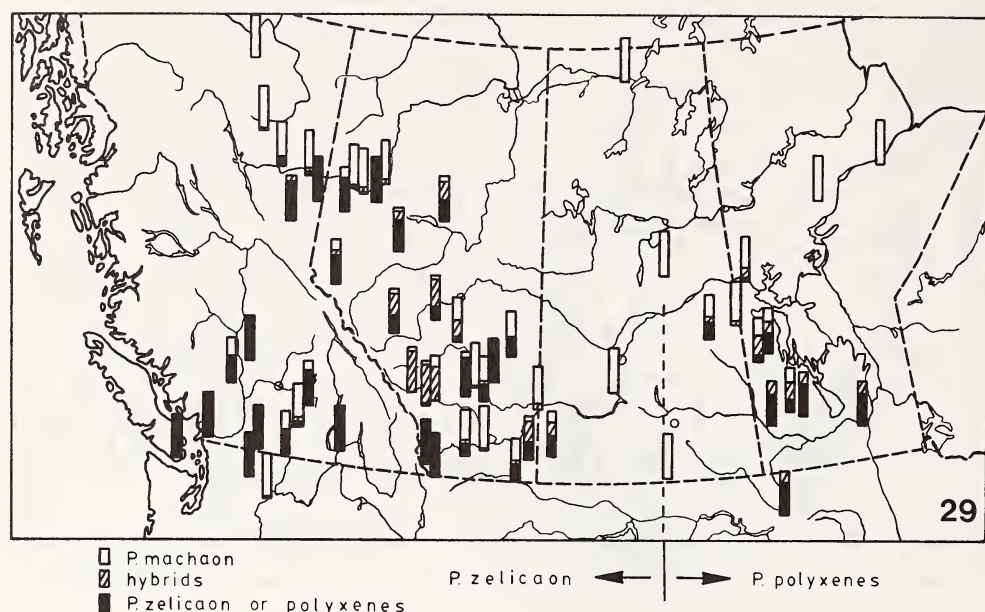
Figure 29. Frequency of interspecific hybrids in western Canada.

Papilio machaon occurs in most of the available major vegetation zones in western Canada (Figures 30 and 31), as shown by relating long term records for temperature and precipitation (Canadian Climate Normals, 1951–1980. [1982a and 1982b]) for weather stations close to localities at which specimens have been collected. These show a clear pattern of differing habitat use among the subspecies of *P. machaon*, as well as between *P. machaon* and the other two species (Figure 32 and 33).

P. m. dodi, *P. m. oregonius* and *P. m. pikei* are most common in patchy populations in dry valley bottoms and slopes of river banks or badlands. They are replaced by *P. zelicaon* at higher altitudes and in moister habitats (*e.g.*, McDunnough, 1927), though males of the two species are occasionally collected together on hilltops immediately surrounding dry valleys. *P. m. aliaska* is replaced by *P. zelicaon* in forested areas south of the Peace River, although *P. zelicaon* is not a resident in alpine habitats and only a few individuals fly to the tops of the lower mountains. According to Freeman (1972), the northern populations of *P. machaon* are also absent from areas with acidic granitic formations.

In contrast to the situation within *P. machaon*, populations of *P. zelicaon* are relatively continuous, with no evidence of any major disjunctions within the species (Figure 27). *P. zelicaon* occurs in broad sympatry with *P. machaon*, with a frequency of less than 5% of natural hybrids in much of western Canada (Figure 29), but large hybrid populations occur in south and central Alberta.

The Cypress Hills of southeastern Alberta and southwestern Saskatchewan contain one major hybrid population (Figures 28 and 29). *P. zelicaon* is found on the partially wooded and prairie hills surrounding the plateau, sometimes together with *P. m. dodi*, but both species merge into a hybrid population in the more heavily wooded central areas. The "Cypress Hills

Old World Swallowtail" (misidentified as *P. m. dodi*) of Hooper (1973), most likely refers to this hybrid swarm material.

A much larger series of hybrid populations is in central Alberta – probably the result of genetic swamping of a *P. m. hudsonianus*-like population which once existed in this region (Figure 42 and 44). *P. zelicaon* abruptly replaces the hybrid swarm populations west of the easternmost slope of the Rockies in Alberta, as well as south of the Crowsnest Pass. Near Lesser Slave Lake, at the northern edge of the central Alberta hybrid swarm, hybrid specimens form 20 to 40% of the total population at any one locality. This frequency increases toward the south and reaches a maximum west of Calgary, where specimens assigned as hybrids comprise more than 90% of the total populations (Figure 29). I have noticed no difference in habitat between individuals which are the most *P. zelicaon*-like, and those which are the most *P. machaon*-like ("nr. *hudsonianus*" in Figure 26). Almost all the localities at which hybrid populations are found occur between 1000 and 2000 m elevation in central Alberta, while localities recorded for *P. m. dodi* are below 1100 m (Figure 11). Hybrid forms are less common farther south and east of Calgary, probably because the foothills and mixed forest habitat they occupy is greatly reduced in extent. A few hybrid specimens from Bragg Creek and Buck Lake seem likely to have been derived in part from *P. m. dodi*. These adults have the long tails and pointed forewings which usually distinguish *P. m. dodi* from both *P. m. hudsonianus* and *P. zelicaon*.

P. polyxenes occurs in Manitoba, where the species fills part of the gap between boreal *P. m. hudsonianus* and prairie *P. m. dodi* and *P. zelicaon* (Figures 26 and 27). *P. polyxenes* X *machaon* populations from central Manitoba occupy a habitat very similar to that of *P. zelicaon* X *machaon* populations from central Alberta (Figures 28 and 33).

The hybrid populations in central Manitoba are for the most part isolated from the main range of *P. m. hudsonianus* and may be in the process of being swamped by *P. polyxenes* in the area, along with the remnants of *P. m. hudsonianus*. Most typical *P. m. hudsonianus* adults were collected in Riding Mountain Park in the 1930's and 1940's, at which time they appeared to form about half of the catch of local collectors. By 1955 *P. m. hudsonianus* was already quite uncommon (Remington, 1956), and in the mid 1970's it was certainly very rare (Heron and Robinson, 1976). Intermediate black morph adults also may be becoming less common, since they were at least as common as more typical *P. polyxenes* in the 1930's to 1950's, but have formed a lower proportion of the total catch in the last two decades. As well, specimens closer to the typical appearance of *P. p. asterius* are more common in the farmland, which surrounds Riding Mountain Park completely and Duck Mountain Park on three sides. Hybrid specimens are very rare north of Duck Mountain Park (Figure 16). The changing status of the hybrid populations in central Manitoba is a major reason for retaining the established taxonomic practice of recognizing these taxa as separate species.

P. p. asterius is very uncommon in southern Saskatchewan, and so there is little contact with *P. zelicaon* in Canada. In Colorado, *P. polyxenes* occurs at lower altitudes than *P. zelicaon*, though these two species meet and occasionally hybridize along a broad zone of contact (Remington, 1968b; Fisher, 1980; Scott, 1981). In Missouri, *P. polyxenes* completely surrounds the range of *P. joanae*, and apparently these two species are reproductively isolated, in part by habitat preferences (Heitzman, 1973). Since *P. polyxenes* and *P. joanae* are distinguished by very few morphological characteristics, this contention of isolation is clearly in need of confirmation. Since the problem has not been investigated in the present study, I follow current practice (Opler and Krizek, 1984), and refer to *P. joanae* as a separate species.

Table 10. Flight periods in western Canada

X = peak, + = reduced numbers, - = rare, ? = questionable record.

Taxon	April	May	June	July	August	September
P. machaon aliaska		-	+ - X X X X	X X + + + - ?	? ? ?	
P. machaon hudsonianus		-	- + X X X	X + + - ?	?	?
P. machaon pikei		- X X	X + + + +	+ +	- +	
P. machaon dodi		+ +	+ - - + -	- + X X	X +	-
P. machaon oregonius	-	- -	- - - -	- -		
P. zelicaon X machaon - central Alberta		- +	X X X + +	+ + + +	-	
P. zelicaon X machaon - Cypress Hills		- -	- + + X	+ + X	-	
P. zelicaon - southern British Columbia	+	- X +	+ + + X +	+ + +	-	-
P. zelicaon - Peace River region		- +	+ X + +	+ +	- -	
P. zelicaon - southern Alberta prairie	- + +	+ X	- - - -	- - -	- -	-
P. zelicaon - southern Alberta mountains	? ?		- X - X	X +		
P. polyxenes X machaon - Manitoba		- -	X X X X +	+ - - -	- -	-
P. polyxenes asterius - Manitoba		+ +	X X X +	- + +	- -	-
Bragg Creek: nr. P. machaon		-	- +	- -		
P. zelicaon X machaon		+ -	X X X +	- +	-	
nr. P. zelicaon		-	+ + -	- - -	- -	-
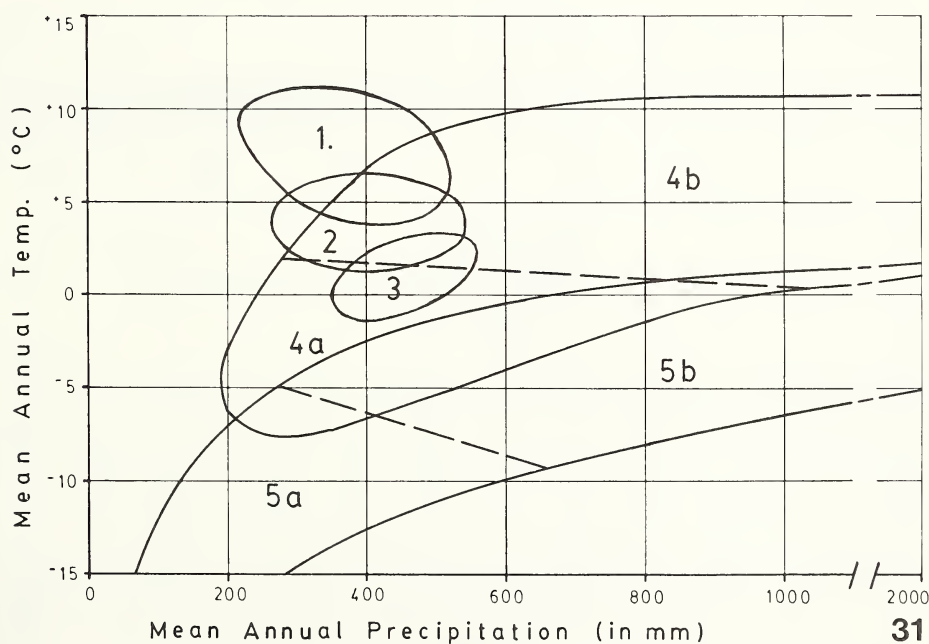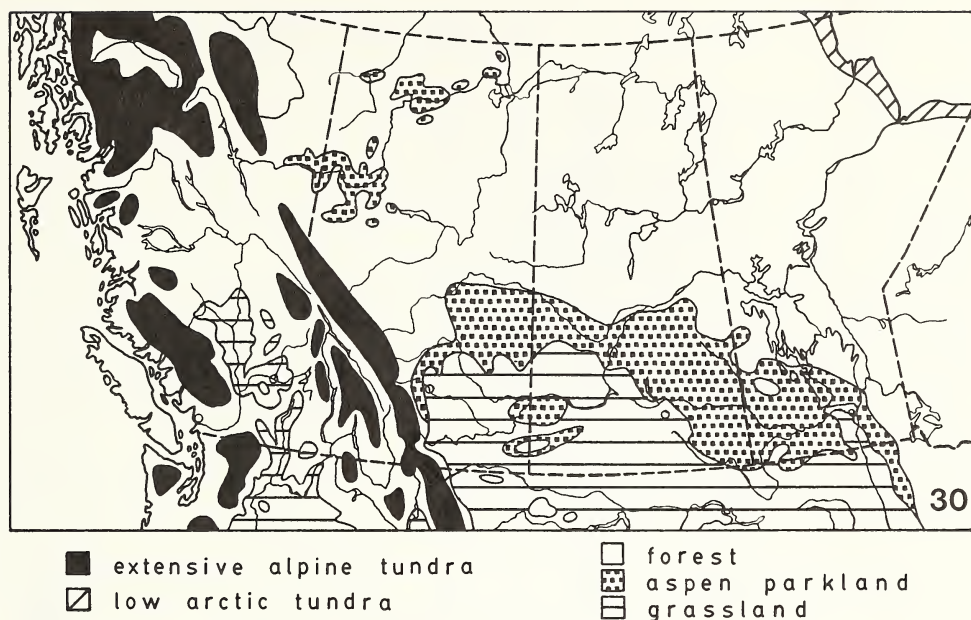
Figures 30 and 31. Figure 30. Major vegetation zones in western Canada Figure 31. Mean annual temperature and precipitation of major vegetation zones Canadian Climate Normals, 1951-1980 (1982a and 1982b). 1, Grassland in southern British Columbia. 2, Grassland in southern Alberta and Saskatchewan. 3, Aspen parkland of Alberta to Manitoba. 4a, Boreal forest of northern British Columbia to Quebec. 4b, Forest of south and central British Columbia. 5a, Arctic tundra of Northwest Terr. to Quebec. 5b, Alpine tundra of Alberta, British Columbia and Yukon Territory.
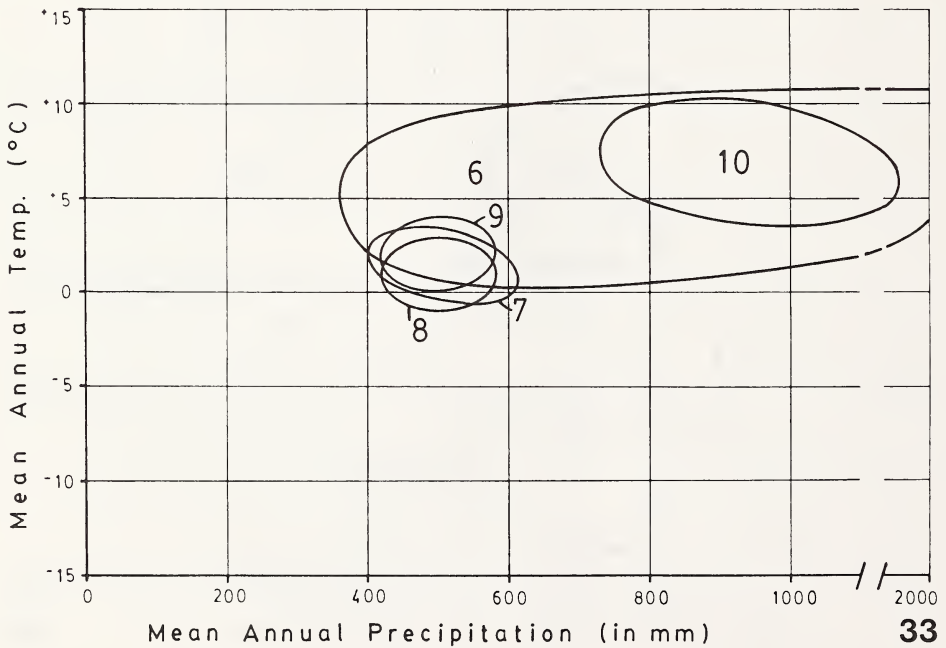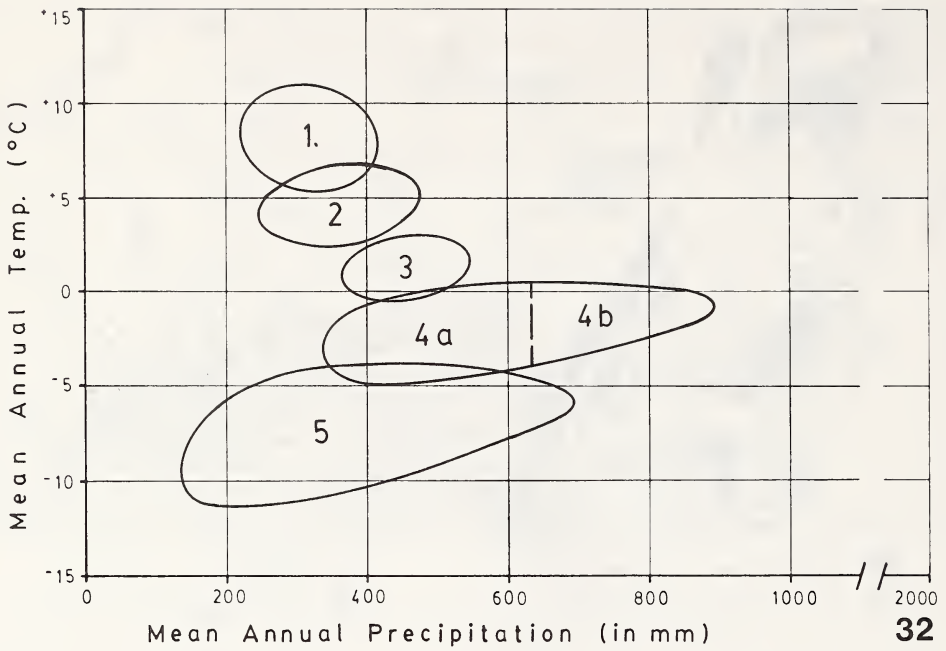
Figures 32 and 33. Figure 32. Occurrence of *P. machaon* subspecies vs. mean annual temperature and precipitation: 1, *P. m. oregonius* in southern British Columbia. 2, *P. m. dodi* in southern Alberta and Saskatchewan. 3, *P. m. pikei*. 4a, *P. m. hudsonianus* in Alberta to Manitoba. 4b, *P. m. hudsonianus* in Ontario and Quebec. 5, *P. m. aliaska*. Figure 33. Occurrence of *P. zelicaon* and *P. polyxenes* vs. mean annual temperature and precipitation 6, *P. zelicaon* in Alberta and British Columbia; 7, *P. zelcaon* X *machaon* in central Alberta; 8, *P. polyxenes* X *machaon* in central Manitoba; 9, *P. p. asterius* in southern Manitoba; 10, *P. p. asterius* in eastern Canada.
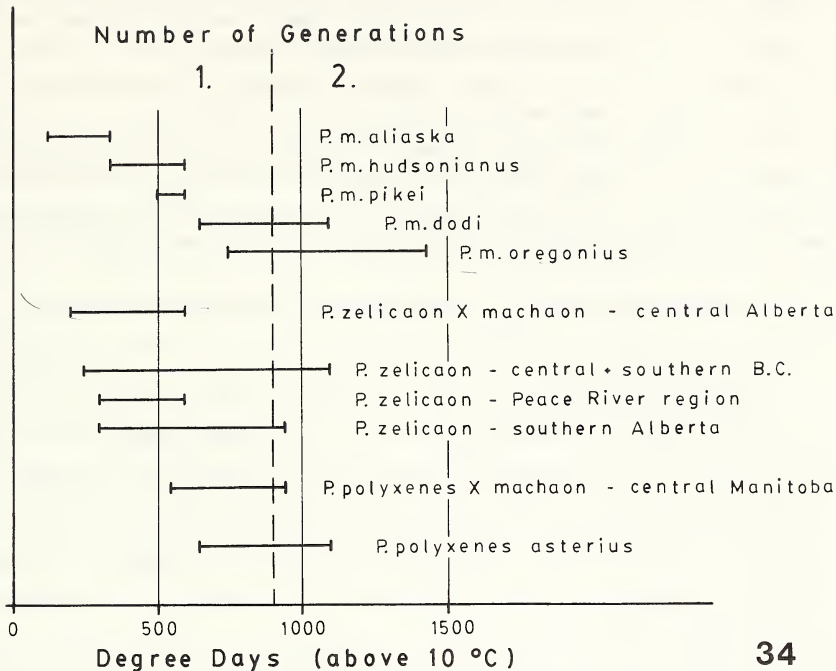
Figure 34. Relationship between voltinism and degree days. Bars show range of degree days (above +10 C) to which *P. machaon* group taxa are exposed in western Canada. Data are taken from weather stations near collection localities (Canadian Climate Normals, 1951-1980. [1982c]). Dashed line indicates approximate number of degree days above which populations have a partial second brood.

Phenology

Variation in flight period and voltinism in the *Papilio machaon* group is primarily geographic and within species. *P. machaon*, *P. zelicaon*, and *P. polyxenes* each include a variety of different populations which range from strict univoltinism to multivoltinism, and have a flight period for adults which ranges from a few weeks per year to an almost or completely continuous emergence (Blau, 1981a, 1981c; Dornfeld, 1980; Emmel and Emmel, 1973; Fisher, 1980; Wiklund, 1973; Wiltshire, 1958). The remaining species in the *P. machaon* group also have fairly flexible phenologies. Some populations of *P. indra* and *P. hospiton* are partially bivoltine (Fisher, 1980; Kettlewell, 1955). These two species and *P. alexanor* may have a very extended emergence period, depending on climatic conditions, and some pupae of *P. indra* and *P. alexanor* have remained in diapause for several years (Fisher, 1980; Nakamura and Ae, 1973). Since most species in the *P. machaon* group exhibit labile phenological responses to different habitats, the genetic potential to adjust in these ways is probably plesiotypic (ancestral) within the species group.

Phenological variation in the *P. machaon* group species is less pronounced in western Canada (Table 10), perhaps due to a more limited range of habitats. *P. machaon* and *P. zelicaon* are strictly univoltine in the northern regions of western Canada, and have a large second generation in the warmer southern regions (Figure 34). Partial bivoltinism is more widespread in southern *P. machaon* than in *P. zelicaon*, probably because the *P. machaon* populations occupy warmer habitats. *P. polyxenes* is at least partly bivoltine through most of its range in western Canada, but also shows a marked decrease northward in the size of the second generation, even though it occupies the relatively warm agricultural areas. The main flight period tends to occur slightly later in the year at higher altitudes and latitudes for all three species.

Although *P. zelicaon* adults tend to emerge slightly earlier in the season than those of *P. machaon* where these species are sympatric, the amount of overlap in flight period is still very large and cannot account for any interruption in gene flow between the species. A substantial amount of overlap in flight periods is also true of *P. machaon* and *P. polyxenes* in Manitoba.

Voltinism of *P. machaon* group populations is related to growing temperatures in western Canada. Figure 34 shows the approximate range of degree days above 10 C (Canadian Climate Normals, 1951–1980. [1982c]) to which these different populations are exposed. Populations which have some adults emerging in a second brood occur in areas receiving approximately 900 or more degree days per year. This contrasts with the situation in *P. glaucus*, in which the potential for multivoltinism appears in populations from areas receiving more than 1200 degree days per year (Scriber, 1982).

Despite similarities among related species with respect to phenologies, many artificial interspecific hybrids in *Papilio* show unusual characteristics of adult emergence. These can be relatively pronounced even when both species are within the same species group (Clarke *et al.*, 1972 and Oliver, 1969), as well as when they are more distantly related (Shimada, 1979). Natural hybrids of the *P. machaon* group in western Canada usually fly at the same time as the main flight of the parental species. However, several interesting exceptions are noted. In the grasslands of both the Peace River region and southern Alberta, where hybrids are rare, the latest record for any *P. machaon* group individual is for a hybrid specimen.

In central Manitoba, *P. p. asterius* has a partial second brood, while *P. m. hudsonianus* is univoltine. Some black morph individuals of *P. polyxenes* X *machaon* have been collected during the second brood flight period, but yellow morph hybrid individuals are only known from the first brood. This provides evidence, independent of similarities in color pattern, that yellow morph hybrids represent only the most *P. m. hudsonianus*-like proportion of the central Manitoba hybrid populations.

In central Alberta, the most *P. machaon*-like and the most *P. zelicaon*-like individuals generally fly in about the same proportions through most of the flight period. However, at Bragg Creek *P. zelicaon*-like individuals occur at low frequency throughout the flight period, but include the only two specimens collected as late as mid August (Table 10). The most likely explanation for the occurrence of these individuals is that they have dispersed in from the more typical *P. zelicaon* populations in the mountainous Kananaskis area immediately to the west. Since most of the *P. zelicaon* adults west of Bragg Creek fly at least a month later than hybrid populations at Bragg Creek, there is a partial temporal isolation of these hybrid populations from the parental species.

Although phenological variation within species of the *P. machaon* group grades clinally from one region to another and is generally not useful for making taxonomic distinctions, *P. m.*

pikei shows some distinctive features. It differs from southern *A. dracunculus*-feeding *P. machaon* subspecies in that *P. m. pikei* is strictly univoltine, while some proportion of these southern populations emerges as a second generation. These differences are maintained when larvae of these subspecies are reared together in the laboratory. Also, adults of *P. m. pikei* emerge a relatively long time after the onset of warm temperatures, compared to *P. m. dodi*, *P. m. oregonius* and *P. m. aliaska*. This difference in emergence time is especially noticeable considering that *P. m. dodi* adults are out early in the flight periods of such species as *Oeneis uhleri* Reakirt and *Papilio glaucus* L. in southern Alberta, but *P. m. pikei* adults do not fly until the main flight of these species in the Peace River region. A possible explanation for this is that the short growing season in the Peace River region provides strong selection against bivoltinism, while larval foodplants are more abundant or palatable later in the season.

Larval Food Plants

Larvae of the *P. machaon* group feed on a variety of species of Umbelliferae, Rutaceae and Compositae (Berenbaum, 1981; Emmel, 1975; Emmel and Shields, 1980; Higgins and Riley, 1970; Wiklund, 1974). Umbellifers are the most commonly recorded foodplants, though larvae of most species can feed opportunistically on rutaceous plants, and some populations of *P. machaon* have switched to composites. Within a restricted area, however, most larvae of a species are found only on one or a few species of foodplant.

The ability to feed on rutaceous plants is widespread in the Papilioninae, and particularly in the genus *Papilio* (Ehrlich and Raven, 1964; Richard and Guédeès, 1983; Miller, 1986). Umbellifer-feeding species are restricted to *Papilio*, and are concentrated in the *P. machaon* group. Miller (1986) postulated that Rutaceae-feeding and Umbelliferae-feeding traits each arose at least three times in *Papilio*. On the other hand, the composite-feeding habits of *P. machaon* larvae are unique within *Papilio*. For the *P. machaon* group, I consider the composite-feeding habit to be the most derived trait, with umbellifer-feeding ancestral. The common ancestor probably evolved from Rutaceae-feeding stock, and Rutaceae-feeding habits have occurred as opportunistic reversals in several species of the *P. machaon* group.

Of the latter, larvae of *P. machaon* feed on the greatest range of foodplants. Records for Eurasian larvae of this species are mainly from umbellifers, less commonly from rutaceous plants, and only accidentally from plants of other families. An important exception occurs in northwestern Afghanistan, where Müting (1972) found mature larvae of *P. machaon centralis* Staudinger on "Wermutstrauchern" (*Artemisia absinthium* L.: Compositae). Larvae of North American subspecies of *P. machaon* appear to feed almost exclusively on composites, and particularly on plants of *Artemisia* (Figure 35 and 36). This contrasts with *P. machaon* populations from northeastern Siberia, which often occur in similar habitats, but for which Kurentzov (1970) mentions only various umbellifers as larval foodplants. Details about occurrence of larvae on foodplants are provided by Sperling (1986).

The only two records for wild-collected larvae of *P. m. aliaska* from North America are from composites (Table 14). Several other foodplant records for *P. m. aliaska* refer to ovipositions observed on *A. arctica* plants. A few larvae of *P. m. aliaska* may feed on umbellifers in nature (Kimmich, 1979), but no larvae have as yet been collected on umbellifers.

A single record of a wild-collected larva is known for *P. m. hudsonianus* (Table 14). I have seen a photograph by G. Anweiler of a freshly molted fifth instar larva resting on a leaf of *Petasites palmatus* (Compositae), with feeding signs on the side of the leaf. The plant represented a different variety of the same species on which Bryant found *P. m. aliaska* larvae
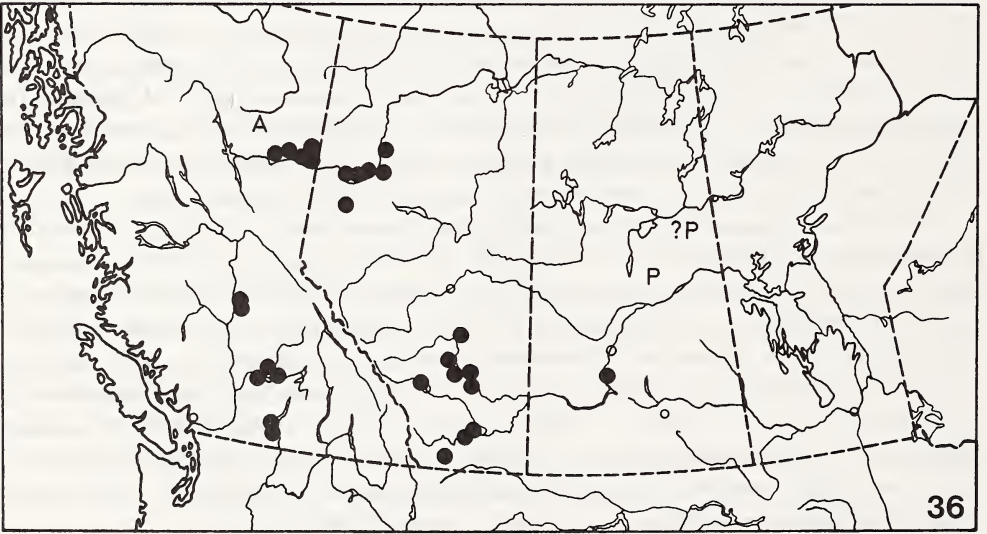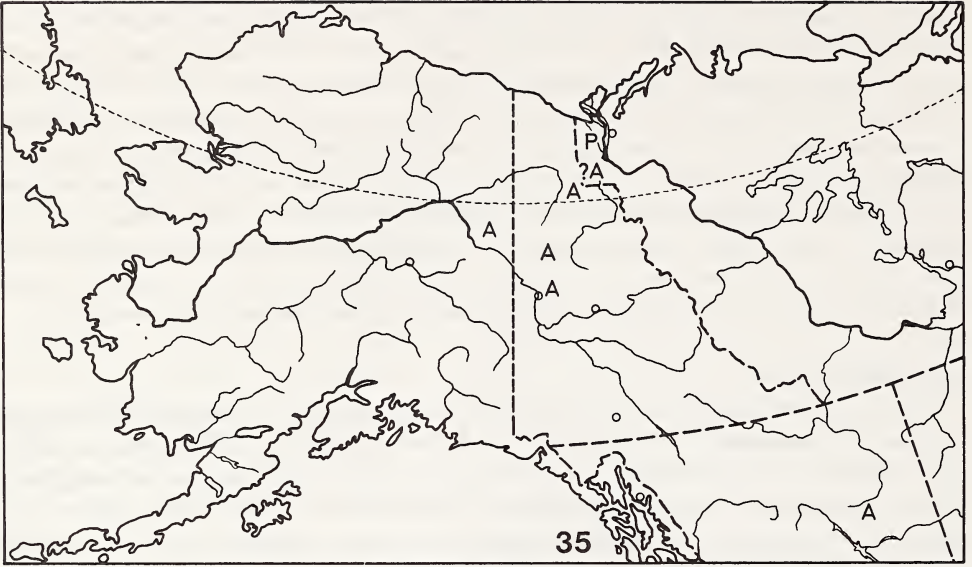
Figures 35 and 36. Locations of larvae collected on composites: A = *Artemisia arctica* Less; black dots= *Artemisia dracunculus* L.; P = *Petasites palmatus* (Ait.) Gray. Figure 35. *P. machaon* larval records – Alaska and Yukon Territory. Figure 36. *P. machaon* larval records – Western Canada.

at Aklavik (Leussler and Bryant, 1935). Anweiler also observed oviposition by *P. m. hudsonianus*, which was reported by Hooper (1973) as being on black snakeroot (Umbelliferae), but the record could just as well refer to *Petasites palmatus* (R. Hooper, *in litt.* 1981).

Many larvae of the *P. machaon* group have been found on plants of *Zizia aptera* (Umbelliferae) in central Manitoba. Though most of these developed into black morph adults (*P. p. asterius* or *P. polyxenes* X *machaon* hybrids), about 2% of them produced yellow adults similar to *P. m. hudsonianus* (*in litt.*, J. Troubridge). However, the yellow adults differed from typical *P. m. hudsonianus* in showing a basally darkened, *avinoffi*-like wing pattern that suggested they were hybrids with *P. polyxenes*. I have also reared adults very similar to *P. m. hudsonianus* from *P. zelicaon* X *machaon* hybrid populations at several localities on the east slope of the Rockies in Alberta. The foodplants included *Z. aptera* at Bragg Creek, and *H. lanatum* at Buck Lake and Nordegg.

Although the southern subspecies of *P. machaon* have previously been considered to be specifically distinct from *P. m. aliaska* and *P. m. hudsonianus*, it is clear that the differences in larval foodplant between these taxa are relatively small. Larvae of *P. m. pikei*, *P. m. oregonius*, *P. m. dodi*, and *P. m. bairdii* are all restricted to a single species of Compositae, *Artemisia dracunculus* (Table 14). Many larvae of *P. machaon* collected on *A. dracunculus* feed on umbellifers if they are transferred to them (Edwards, 1893, 1898; Emmel and Emmel, 1963; J. Troubridge, *in litt.* 1981; personal observation, 1982; but contrast Newcomer, 1964). However, mortality of these larvae is high on most umbellifer species. Larvae of *P. zelicaon* and *P. polyxenes*, for their part, do not feed on *A. dracunculus*.

P. zelicaon larvae feed on rutaceous plants as well as on a wide variety of umbellifers in the United States, and *Angelica* species seem to be especially favored (*e.g.,* Emmel and Shields, 1980). In contrast, *P. indra* larvae are found on a narrower range of umbellifers, particularly *Lomatium* species (Emmel, 1975). Although largely separated by habitat, some *P. zelicaon* larvae feed on the same species of foodplants as those used by *P. indra* larvae.

In California, *P. zelicaon* larvae feed frequently on the introduced weedy umbellifer, *Foeniculum vulgare* Mill., and in some localities feed on *Citrus* (Rutaceae) orchards (Shapiro and Masuda, 1980). The foodplant shift to recently introduced umbelliferous and rutaceous plants has allowed *P. zelicaon* to produce several broods a year on these host plants, rather than the single brood that is normally possible on native umbellifers (Emmel and Shields, 1980; Sims, 1980 and 1983). Remington (1968a) considered larval foodplant preferences as evidence for the specific distinctness of his *P. gothica*. However, the foodplant preferences he listed have been disputed by Emmel and Shields (1980). I have confirmed the findings of the latter authors by obtaining larvae from plants of *Angelica ampla*. One larva was reared to the adult stage.

In western Canada, only umbelliferous foodplants are known for larvae of *P. zelicaon* (Table 14, Figures 37 and 38). *Heracleum* plants are used commonly, though *Angelica* plants tend to be used more frequently at localities where these plants are more numerous. Although plants of *Artemisia arctica* and *Heracleum lanatum* grow together near treeline at many sites in the Peace River region, this does not seem to promote hybridization between *P. zelicaon* and *P. m. aliaska*.

Larvae of *P. zelicaon* X *machaon* populations in central Alberta also feed on umbellifers. At Bragg Creek, these populations show some segregation from *P. zelicaon* populations to the west and south, and the larvae feed mainly on plants of *Zizia*. In the northern part of central Alberta, the hybrid populations merge into typical *P. zelicaon*, and the larvae feed on
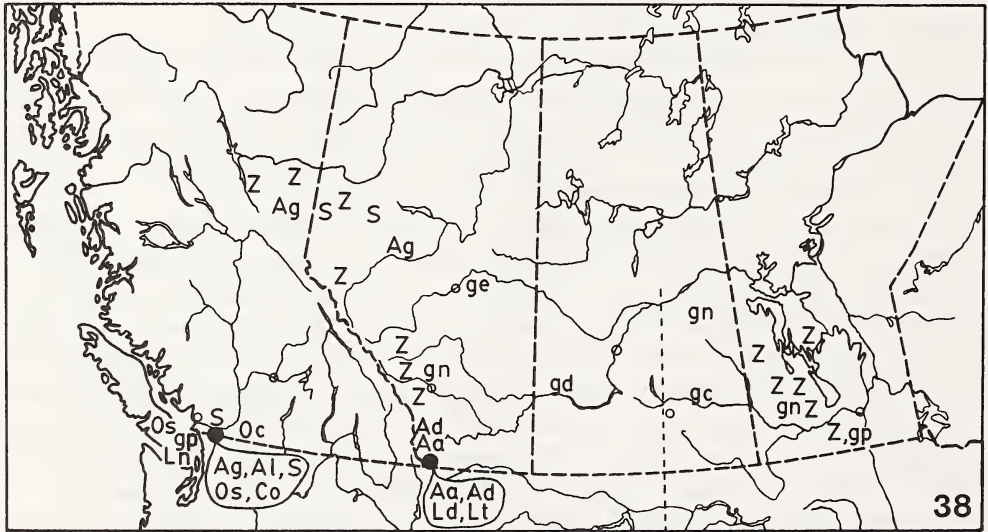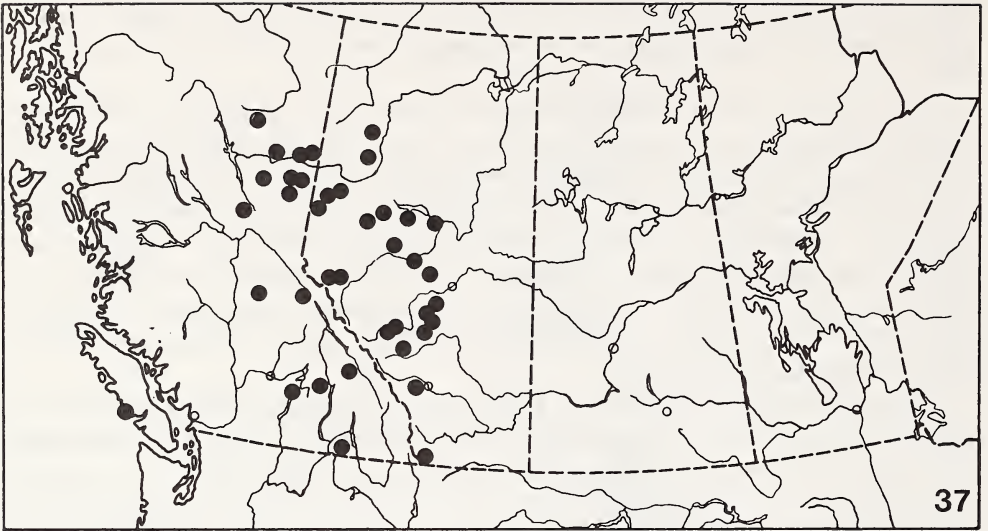
Figures 37 and 38. Locations of larvae collected on umbellifers. Figure 37. Larvae collected on plants of *Heracleum lanatum* Michx. Figure 38. Larvae collected on other umbellifers. Aa = *Angelica arguta* Nutt.; Ad = *Angelica dawsoni* S.Wats.; Ag = *Angelica genuflexa* Nutt.; Al = *Angelica lucida* L.; Co = *Cicuta occidentalis* Greene; Ld = *Lomatium dissectum* (Nutt.) Mathias & Constance; Ln = *Lomatium nudicale* (Pursh) Coult. & Rose; Lt = *Lomatium triternatum* (Pursh) Coult. & Rose; Oc = *Osmorhiza chilensis* Hook. & Arn.; Os = *Oenanthe sarmentosa* Presl.; S = *Sium suave* Walt.; Z = *Zizia aptera* (A.Gray) Fern; gc = garden carrot (*Daucus carota*) L.; gd = garden dill (*Anethum graveolens*) L.; ge = garden celery (*Apium graveoens*) L.; gn = garden parsnip (*Pastinaca sativa*) L.; gp = garden parsley (*Petroselinum crispum*) (Mill.)Mansf.

Heracleum plants, a more common foodplant of *P. zelicaon*.

I have obtained black morph adults from two species of Umbelliferae: one, with typical *P. zelicaon* on *Angelica arguta* at Waterton Park, Alberta; others, on *Zizia*, and were part of the hybrid population at Bragg Creek, Alberta. In both groups the black and yellow morph specimens were produced in similar proportions to those of wild-collected adults. Hooper (1973) also reported both black and yellow morphs being produced from the same umbelliferous foodplant: garden dill (*Anethum graveolens*) at Eston, Saskatchewan. As well, I have reared one black morph adult from larvae of *P. m. dodi* , collected on *Artemisia dracunculus* at Taber, Alberta. These observations support the electrophoretic evidence, which indicates that the black adult morph is an integrated part of several taxonomically different *P. machaon* group populations in western Canada.

Larvae of *P. p. asterius* are found on a broad range of umbellifers and even a few rutaceous species (Berenbaum, 1981). Many of these are either introduced or common in cultivated areas, and so the fact that *P. p. asterius* is a common butterfly in much of eastern North America may be a recent phenomenon, aided by human agricultural patterns in the last two hundred years or so (Feeny *et al.*, 1985). Larvae of *P. p. asterius* may occasionally be found on the same species which support *P. joanae* and *P. brevicauda* and so these ecological distinctions between the two species are not major (Berenbaum, 1978; Jackson, 1982; Opler and Krizek, 1984). In desert areas of the southwestern United States, *P. p. coloro* Wright larvae feed mainly on plants of *Thamnosa* species (Rutaceae) (Ferris and Emmel, 1982). In this region *P. polyxenes* is in part sympatric with *P. m. bairdii* (larvae of which feed on *Artemisia dracunculus*), and *P. indra* (larvae of which feed on umbellifers).

As with *P. zelicaon* , the larvae of *P. p. asterius* feed only on umbellifers in western Canada. However, the larvae of *P. p. asterius* frequently use introduced and cultivated foodplant species, while this is more infrequent for *P. zelicaon* larvae. I have examined adult series reared from two introduced foodplant species in Manitoba and Saskatchewan (Table 14). Both of these series contain specimens ranging from typical *P. p. asterius* to at least one which was more typical of the *P. polyxenes X machaon* hybrid populations which are common in forested areas.

In the zone of interaction between *P. p. asterius* and *P. m. hudsonianus* in central Manitoba, the native umbellifer, *Zizia aptera*, is the primary larval foodplant (Figure 38). *Z. aptera* plants are more characteristic of open meadows than forests, and so are not a major factor in the partial habitat separation between hybrid populations of *P. polyxenes* and *P. polyxenes X machaon*. I have not been able to confirm Tyler's (1975) report that cow parsnip (*H. lanatum*[?]) may be a larval foodplant for these populations.

Table 11. Character state distributions within *P. machaon* group taxa

Frequency: X = most common, + = greater than 10%, - = less than 10%
Adult morph.: Letters and numbers correspond to those of characters on Table 2.
Adult electr.: Only alleles with a frequency of more than 10% in at least one taxon are included. Allele letters correspond to those in Table 6. Character polarities not shown due to absence of outgroup information.
Larval: Spot color (sp) = orange (o) & yellow (y). Foodplants (fd.) = Rutaceae (r), Umbelliferae (u) & Compositae (c)
Misc. abbrev.: P = primitive, D = derived, c.AB = central Alberta, c.MB = central Manitoba

CHARACTER SUITE	Adult Morphometric											Adult Electrophoretic								Larval	
CHARACTER NUMBER OR LETTER	A.	B.	C.	D.	E.	F.	G.	H.	I.	J.	K.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
CHARACTER NAME	DHW yel.	DHW pup.	DHW b/r ula	teg ula	VFW disc	VFW tip or.	VHW or.	tho rax	abd.	abd LL	abd UL	GGPD	ID	ME	ODH	E4	E5	P1	P2	sp	fd.
STATE or ALLELE	1234	1234	123	123	1234	123	1234	123	1234	123	1234	abkc	bd	iab	abc	ab	ac	ab	ab	oy	ruc
P. hospiton	+X-	+X	X X	X X	X-	X	X+	X	X	X	.									X	X
Palearctic *P. machaon* ssp.	+X+-	+X	X+-	-X	X-	X	X+	X	X	X	X									X	+X-
P. m. oregonius	-+X+	-X-	X++	X-	X+-	X	+X-	X-	X-	X-	X	- X	X+	++X	-X	X-	+X	X+	+X	X	X
P. m. dodi	+X+	+X+	-X+-	X--	++X	X	+X	X-	+-X	X--	-X	--X	X+	-+X	-X	X-	+X	X+	+X	X-	X
P. m. bairdii	X++	+X+	-+X	X+	-+X	X+	-X-	++X	--X	++X	X+-+	- X	X+	-+X	+X-	X+	-X	X+	+X	X+	X
P. m. pikei	X++	+X-	X+-	X	X	X+	X+	X	X	X	-X	--X	X-	+X	X-	X+	X+	X+	-X	X+	X
P. m. aliaska	X-	X+	X+	X	X-	+X	+X	X-	X	X	+X	-- X	X+	-+X	-X+	X-	-X	X+	-X	-X	X
P. m. hudsonianus	X-	+X-	-+X	X	X--	X	+X	X-	X	X	+X+	-- X	X+	-+X	+X-	X+	-X	X+	-X	X	X
P. zelicaon X machaon -c.AB	X+-	-X+-	-+X-	X-	+++X	-X--	-X--	+X+	+-X	-X-+	-+X	-+-X	X+-	--X	+X-	X+	+X	X+	+X	+X	X
P. zelicaon	X++-	-+X	-X	X-	-+X	-X-	-X-	X+	--X	X--	-X	-X-+	X-	-+X	-X	-X	-X	X-	+X	+X	+X
P. polyxenes coloro	X++-	-+X	X-+X	+X+	X	+X+	+X+	+X	X	+-X	X+--	+- X	X+	++X	-X	X-	+X	X X	XX	?X X-	X
P. polyxenes X machaon -c.MB	X-	+X++	-+X+	+X+	-X	-+X	-+X	-X	--X	X-	X--	+ X	X	-+X	X	X-	+X	X X	XX	-X	X
P. p. asterius	X	-+X	X	+X	-X	X	X	X	-X	X	X	X				X-	X X	X X	X-	+X	-X
P. joanae	X	+X	X	-X	X-	-X	X	X	X	X	X	X+	X+	++X	X-	X-	X	X	-X	-X	X
P. brevicauda	X	-+X	X	X-	X	+X-	X-	X	X	X	X	X X	X+	-+X	X	X X	X	X		-X	X
P.p.polyx.,stabilis &americus	+X+	+X	X	X++	X++	X	X	-X	-X	-+X	X+-	X+	X	++X	X	X+	X	X	-X	X+	-X
P. indra	X-	-+X	-X	X+-	X	-X	X+	X	X	X+	X	X+	X	++X	X	X-	+X	X	-X	X+	X
CHARACTER POLARITY	DPDD	DPPD	DDP	PDD	DPPD	PPDD	PPDD	PDD	PDDD	PDD	DDDP									PD	PPD

Figure 39. Reconstructed phylogeny of *P. machaon* group. Location of numbers shows hypothesized first appearance of derived states. Letter and number codes are the same as on Tables 2 and 11. Dots on lines represent spread of modifier gene for black wing morph. Widely spaced dots indicate low proportion of black morph individuals or incompletely linked gene combinations. Abreviations: c.AB = central Alberta; c.MB = central Manitoba; 1, B1, C1, E1; 2, A1, B4, E4, H2, I4; 3, 10c; 4, no autapotypies among characters analyzed; 5, D3, F3, G4, H3, J3, K1.

EVOLUTIONARY HYPOTHESES
Origin and Early Differentiation of the *P. machaon* Group

Outgroup relationships of the *P. machaon* group are uncertain. Monroe (1961) did not resolve its affinities to other species groups of *Papilio*, but associated it with the *P. xuthus* group, and suggested that these two groups had affinities with the *P. demoleus* and *P. anactus* species groups. Ae (1979) suggested that the *P. machaon* group was about as closely related to the *P. xuthus* group as it was to the *P. paris* group, which Monroe did not include in his reconstructed phylogeny. Ae also showed that the affinities of the *P. machaon* and the *P. demoleus* groups were probably still more distant. Hancock (1983) ranked the *P. machaon* group as a distinct genus with only ancestral relationships to most of the remainder of the Papilionini. He also suggested that *P. alexanor* represented a lineage predating a split between the *P. machaon* group and more than half of the species groups in the Papilionini.
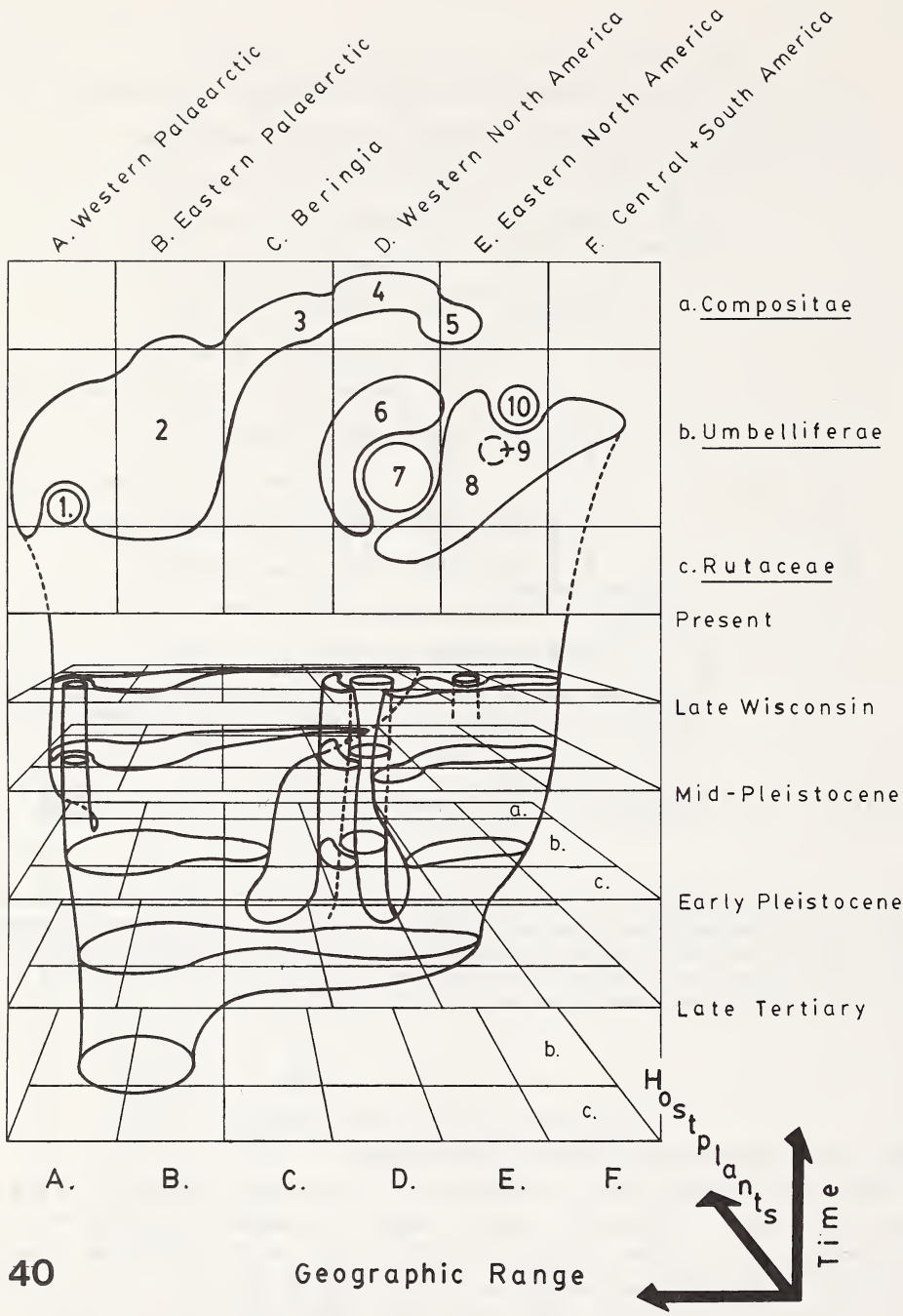
Figure 40. Changes in geographic range and larval hostplants over time: 1, *P. hospiton*; 2, Palearctic *P. machaon* ssp.; 3, *P. m. aliaska*; 4, *A. dracunculus*-feeding ssp. of *P. machaon*; 5, *P. m. hudsonianus*; 6, *P. zelicaon*; 7, *P. indra*; 8, *P. polyxenes*; 9, *P. joanae* (not shown in Late Wisconsin); 10, *P. brevicauda*.

Since adults of *P. alexanor* have a very different, and probably plesiotypic, color pattern and male genitalia, that species must have diverged early from the remainder of the *P. machaon* group. In fact, its inclusion in the *P. machaon* group on the basis of larval characters is so clearly contradicted by adult characters, that I consider it with some caution in my discussion of the phylogeny of the *P. machaon* group.

Because relationships of the *P. machaon* group are uncertain, it is difficult to determine which of its character states are plesiotypic. Seyer (1982) polarized character states by considering genetically dominant traits to have been more recently derived than traits which are more recessive. Since the allele for the black wing morph of *P. p. asterius* is dominant, it was considered derived relative to the yellow morph. On this basis Seyer concluded that *P. zelicaon* was phylogenetically older than *P. machaon*, *P. hospiton* and *P. polyxenes*.

Despite the uncertainty involved in such an undertaking, I offer a hypothesis for the character states of the most recent common ancestor of the *P. machaon* group, excluding *P. alexanor*. My identification of character states as plesiotypic is mainly determined by similarity of these states to those occurring frequently in different possible outgroups. On this basis, the ancestral species was probably similar to present day *P. machaon* though differing in some respects (Table 11), which indicate affinities with either *P. hospiton* or *P. p. americus*. Since none of the possible outgroups occur in the New World, this ancestral species probably lived in the Palearctic region, though it must have dispersed to North America early in the development of the *P. machaon* group.

The ancestral species certainly lived before the Pleistocene, considering the amount of differentiation within the group, though I doubt that the present species in the *P. machaon* group (excluding *P. alexanor*) began to diverge from each other very long before the beginning of the Pleistocene (Figures 39 and 40). Nei's (1972) genetic distance (D) can be a rough indicator of the time of divergence of two lineages, with D increasing by 1.0 every 15–20 million years (Thorpe, 1982:153). Applying this ratio to a value of 0.2 for interspecific comparisons within the *P. machaon* group (Table 7), a divergence time of 4–5 million years is obtained for the three species now occurring in western Canada. For the subspecies within *P. machaon*, divergence times of 0.1 to 1.0 million years are indicated. Although these estimates are imprecise, they nonetheless support the contention that the main lineages of the *P. machaon* group diverged before the Pleistocene, while most evolution within lineages took place during the Pleistocene.

The species which appeared immediately prior to the Pleistocene probably gave rise to four major lineages in the *P. machaon* group, in addition to *P. alexanor*. These lineages include what are now: 1), *P. machaon* and *P. hospiton* ; 2), *P. zelicaon*; 3), *P. polyxenes* , *P. joanae* and *P. brevicauda* ; and 4), *P. indra*. The oldest of these four lineages is probably the one that gave rise to *P. machaon* (Figure 39 and 40). Both *P. hospiton* and *P. machaon* exhibit very few of the apotypic character states of the remaining lineages (Table 11). As well, it is more parsimonious to hypothesize that the *P. machaon* lineage evolved *in situ* in Eurasia, and is not the product of a return dispersal from North America. However, the common ancestor of the remaining lineages probably fragmented soon after colonizing North America. Both electrophoretic characters (Table 7) and hybridization in the laboratory (Ae, 1979) indicate that *P. machaon* , *P. zelicaon* and *P. polyxenes* are approximately equidistant from each other. Also, natural hybridization occurs between each pair combination of these three species, as well as between *P. machaon* and *P. hospiton*.

Relationships of the three lineages which originated in North America are unclear. *P. zelicaon* possesses few if any autapotypic characters, and could conceivably represent the earliest of the three clades to diverge. However, *P. zelicaon* shows little internal differentiation. Although the color pattern of adults of *P. p. asterius* is probably apotypic, *P. polyxenes* contains other races and forms (particularly in *P. p. americus*) which appear to be more plesiotypic. *P. indra* , on the other hand, appears to share some apotypic character states with some subspecies of *P. polyxenes* (Table 11), but shows considerable internal differentiation, and has distinctive adult genitalia and adult and larval color patterns. Though this degree of differentiation may indicate an early divergence time relative to the other species, it may also be a reflection of a different sort of selection regime. In fact, it is conceivable that *P. indra* is so different only because some factor such as distinctive hilltopping behavior (Shapiro *et al.*, 1981) or male genitalia may have allowed it to avoid hybridization and introgression with other species, even though the lineage may be no older than the other three. Since it seems plausible that all three lineages could have diverged at the same time (in West Coast, American southwest, and eastern refugia), I have left this portion of the reconstructed phylogeny as a trichotomy. Further investigations on the species in the American southwest would be important to understanding phylogenetic relationships within the group.

Two main factors contribute to the obscure phylogenetic relationships within the *P. machaon* group. Species with extensive variation and large geographic ranges may simultaneously bud off two or more peripheral populations which are substantially different from each other. Reticulation due to interspecific hybridization is also likely to have been a significant factor in the evolution of the group. For example, the black wing morphs of *P. zelicaon* and *P. machaon* probably result from introgression of genes from *P. polyxenes*, while hybrid populations of two of the three potential combinations are described in this study. Both reticulation and multiple events of peripheral isolation in variable species are likely to produce discordant character distributions, with resultant difficulties in reconstruction of phylogenetic relationships.

Pleistocene Divergences Within Major Lineages

The first dispersal of the *Papilio machaon* group into North America almost certainly took place across the Beringian region between eastern Siberia and Alaska. Land connections through Beringia were intermittent during the Tertiary, and these also formed an intermittent but important biotic dispersal corridor during the Pleistocene (Matthews, 1979).

Large scale glacial advances and retreats that occurred throughout the Pleistocene must have been an important factor in differentiation of new species and races. These glaciations, combined with dramatically altered climates, moved many vegetation associations far south of their present ranges and caused formation of some vegetation associations which have no modern analogs (Matthews, 1982). Glaciations would have displaced populations of the *P. machaon* group a number of times, isolating those in Beringia, and probably fragmenting populations which survived south of the ice in North America.

Distributions of vegetation associations during and after the late Wisconsinan have been fairly well documented. I assume that the habitat associations of most *P. machaon* group taxa have not changed greatly since this time, and thus infer which regions were occupied by these taxa during late Wisconsinan time. Locations of these hypothetical refugial areas are shown in Figure 41, based in part on Scudder (1979:159).

Figure 41. Locations of late Wisconsinan refugia. Continuous lines indicate ice masses. Broken lines show refugia hypothesized for *P. machaon* group taxa in the United States and Canada: 1, *P. m. aliaska*; 2, *P. m. oregonius*; 3, *P. m. hudsonianus*; 3a, *P. machaon* populations similar to *P. m. hudsonianus*, remnants present in *P. zelicaon* X *machaon* hybrid populations in central Alberta; 4, *P. zelicaon*; 5, *P. m. bairdii* and *P. p. coloro*; 6, *P. p. asterius* and *P. joanae*(?); 7, *P. brevicauda*.

Figure 42. Distribution of *P. machaon* in North America. Arrows show hypothesized Holocene dispersal routes.
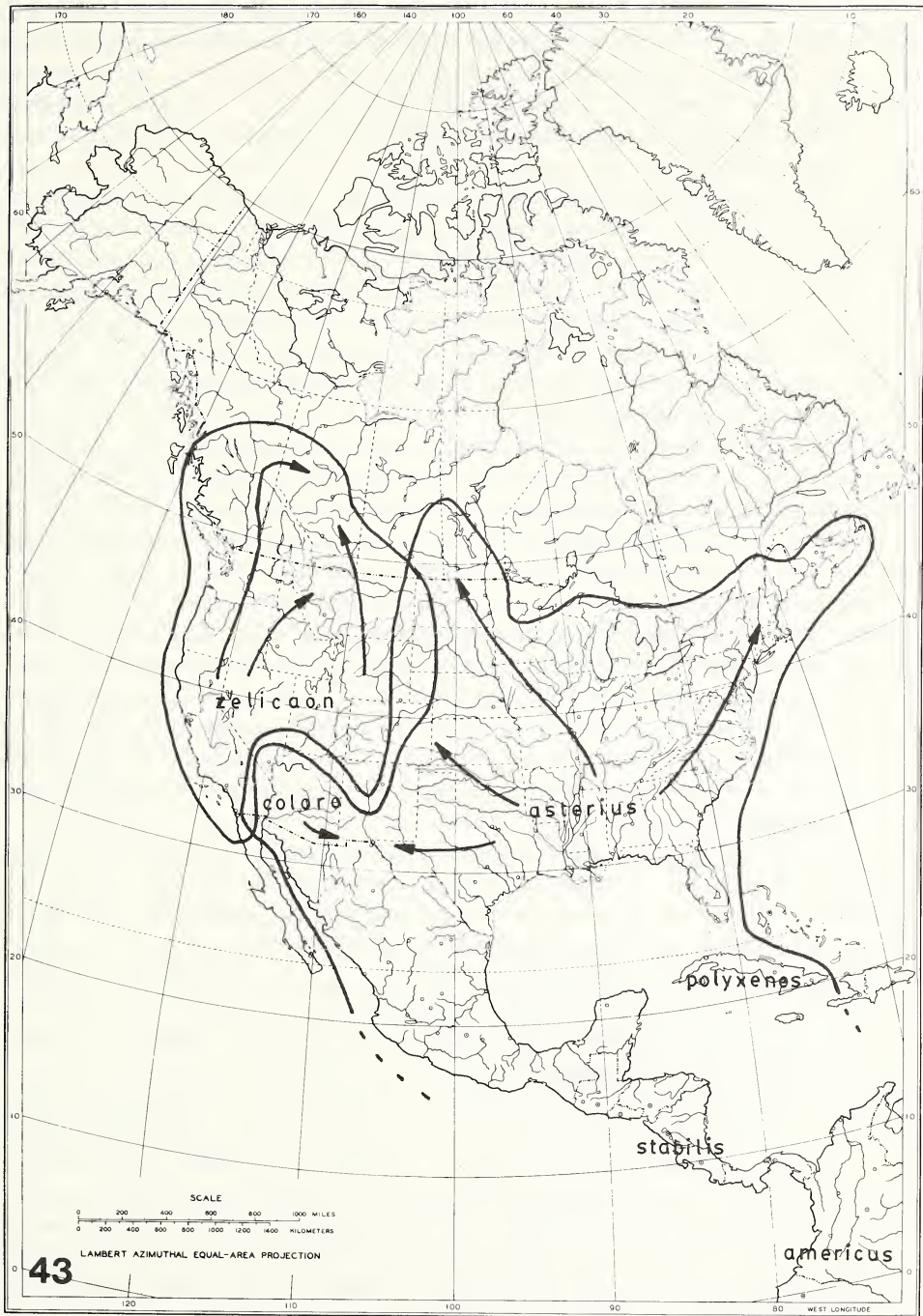
Figure 43. Distribution of *P. zelicaon* and *P. polyxenes*. Arrows show hypothesized Holocene dispersal routes in North America.

The P. machaon lineage.— The *P. machaon* lineage now contains only one species other than *P. machaon* itself. This is *P. hospiton*, which must have become isolated on Sardinia and Corsica very early in the history of the lineage. Rumbacher and Seyer (1979) estimated that this happened during the Mindel glaciation, the second of the four major glacial periods recognized in Europe. The rest of the *P. machaon* lineage occupied most of the Palearctic region, apparently giving little opportunity for populations to develop into anything other than distinct regional races.

The Pleistocene glaciations were probably especially important to acquisition of composite-feeding habits by larvae of *P. machaon* (Figure 40). North America was occupied early in the history of the species group, and so *P. machaon* may have existed for a time in parapatry with the southern species. This kind of replacement may have been similar to that of *P. zelicaon* and *P. polyxenes*, which are presently parapatric over a considerable distance in the western United States. Considering degree of differentiation in the *Artemisia*-feeding subspecies, invasion of western United States by populations with this adaptation must have occurred before the Sangamon Interglacial.

The foodplant shift may have occurred in Beringia, when local populations began to feed on *Artemisia arctica*, a species which is still the main foodplant of Nearctic *P. machaon* in Beringia, and is much more abundant than any umbellifer species in the region. The shift would have been aided by several similarities in secondary plant compounds between plants of the genus *Artemisia* and those belonging to the Umbelliferae (Dethier 1941; Berenbaum, 1983). The plant assemblage of the arctic steppe tundra in Beringia (Matthews, 1982) was probably very similar to that presently occupying the dry, cold climate of northern Afghanistan, the only region in Eurasia in which *P. machaon* has been recorded on *Artemisia*. The later switch of *P. machaon* to *Artemisia dracunculus* in North America may have occurred in Beringia or farther to the south, during a warming trend when Beringian populations came into contact with southern dryland habitats. In any event, the switch to *A. dracunculus* is associated with occupation by *P. machaon* of large regions in sympatry with *P. zelicaon*, *P. indra*, and, in part, *P. polyxenes* (Figures 40, 42 and 43).

A major factor in differentiation of *P. machaon* in North America would have been contact with *P. polyxenes*. Introgression or even more widespread hybridization just after contact with *P. polyxenes* is probably the reason why *P. m. bairdii* acquired the genes for the black morph adult (Figure 39). Support for this suggestion may be derived from the marked similarity between artificial hybrids of *P. machaon* and *P. polyxenes*, and the naturally occurring black morph of *P. m. bairdii*. Though the black morph of *P. machaon* may also be found some distance from the nearest population of *P. p. asterius*, it is restricted to a region where either past contact or allele movement through introgression can account for its occurrence.

During late Wisconsinan time, around 18000 years before present, *P. machaon* must have survived in North America in several different refugia (Figure 41). *P. m. aliaska* would have been restricted to the northernmost refugium, dispersing southward along the Rocky Mountains of northern British Columbia when glacial ice melted. Movements of *P. m. hudsonianus* are postulated with less certainty. The subspecies now ranges to Québec, but is very uncommon west of Saskatchewan. This suggests that it diverged from *P. m. aliaska* before the late Wisconsinan, and occupied the boreal region south of the ice during the last major glaciation (Figure 42).

The stock that *P. m. bairdii* is derived from probably survived in the remnants of desert habitats in the American southwest, and it seems likely that *P. m. oregonius* is derived from a

separate population, suggested by the fact that *P. m. oregonius* has no black form like the one predominant in *P. m. bairdii*. Although most reconstructions of vegetational history show only conifer forest grading into tundra at the edge of the glaciers in the northwestern United States, I suggest that a probable Wisconsinan refugium for *P. m. oregonius* was along the eroding banks of the Columbia River, between Washington and Oregon. Though very close to the ice, the steep north bank of the river must have had a much drier climate than the surrounding region, much like that presently characteristic of the Peace River region. It is even possible that there were dry-tundra adapted *P. machaon* populations along the southern edge of the ice in Washington during the Wisconsinan glaciation, giving rise to *P. m. oregonius* separately from *P. m. bairdii*.

   P. m. dodi is even more problematical, possibly surviving on eroding river banks in the drier areas of the northern Great Plains. However, much of the region was covered by conifer forest, and if *P. m. hudsonianus* also survived south of the ice, it would probably have had some contact with *P. m. dodi*, and yet the latter has a distinctively darker wing and body coloration. A more likely alternative is that *P. m. dodi* did not exist as a distinctive population during late Wisconsinan time. The dark adult coloration could have arisen through hybridization of *P. m. oregonius* and *P. m. bairdii* when these two populations contacted each other during the Holocene (Figure 39). A second explanation is introgression from *P. zelicaon* in founding populations of *P. m. dodi*, but since there is no evidence for it in electrophoretic characters, this is less likely.

   P. m. pikei probably had a separate origin from the *A. dracunculus*-feeding subspecies which range into the western United States. Although almost all of the butterfly species living with it in the Peace River grasslands are clearly derived from conspecific populations in southern Alberta, (E.M. Pike and F.A.H. Sperling, unpublished), *P. m. pikei* is less like *P. m. dodi* than any other subspecies of *P. machaon* in western Canada. *P. m. pikei* shows a much greater phenetic similarity to populations of *P. m. oregonius* living in southern British Columbia. However, it is unlikely that *P. m. pikei* has been derived from *P. m. oregonius* since evidence available from pollen cores (*e.g.,* Hanson, 1949, 1950, 1955; Valentine *et al.*, 1980; White and Mathewes, 1982) does not suggest that the grassland vegetation of interior British Columbia extended across the Rocky Mountains during the Holocene. Thus it is unlikely that *P. m. oregonius* was able to reach the Peace River area.

   I believe it likely that *P. m. pikei* differentiated during the Holocene from *P. m. aliaska*. If larger size and more pointed wings are considered as recent adaptations convergent with other ecologically similar races of *P. machaon* then the greatest morphometric similarity is with *P. m. aliaska*, or perhaps *P. m. hudsonianus*. *P. m. pikei* has an unusual combination of electrophoretic character states, perhaps due to sampling error or genetic drift in the original colonists, but is slightly more similar to *P. m. aliaska* than to any other *P. machaon* subspecies (Table 7). The most westerly populations of *P. m. pikei* presently live about 25 km from the nearest alpine populations of *P. m. aliaska*.

   The most likely time of divergence for *P. m. pikei* is between 8000 and 11000 years B.P. The ice-free section of the foothills east of the Rockies had a periglacial climate at about 11,250 B.P., which was dominated by *Artemisia* and grasses (Schweger *et al.*, 1981). However, between 9000 and 6000 B.P. the climate was much hotter and drier than at present, allowing a major expansion of grassland habitats. The relatively rapid shift from dry tundra to hot grassland may have been an important factor in the differentiation of *P. m. pikei* on the Peace River grasslands.

P. zelicaon and hybrids.— *P. zelicaon* represents a lineage similar in age to the *P. machaon* and *P. polyxenes* lineages, and yet shows much less tendency toward the development of geographic races. The reason for this may be that its range has not been fragmented much by Pleistocene glaciations and habitat changes. *P. zelicaon* probably occupied a large proportion of the western United States even during the late Wisconsinan maximum (Figure 41), and its range may have bisected that of the *A. dracunculus*-feeding populations of *P. machaon*

During the post-Wisconsinan climatic amelioration, *P. zelicaon* would have expanded its range into western Canada from two separate directions (Figure 43). One dispersal route was along the foothills and edge of the Great Plains, and brought genes for the black morph to the prairies and southern foothills of Alberta. The other disperal wave occupied all of British Columbia and spread into Alberta through low mountain passes. It colonized the Peace River region and the northern part of central Alberta.

The two-pronged dispersal of *P. zelicaon* into Alberta seems to have effectively isolated a pre-existing population of *P. machaon* in the foothills of central Alberta. Since most remnants of this population presently live in forested areas south of Cadomin, the population probably was not associated with the alpine refugium discussed by Pike (1980). This *P. machaon* population came in direct contact with *P. zelicaon* on all sides and may have had a relatively low population density, much like *P. m. hudsonianus* populations in northern Saskatchewan and Manitoba. A significant number of individuals must have begun to hybridize with those of invading *P. zelicaon* and eventually formed hybrid populations along the ecotone between montane and boreal forest in central Alberta.

In central Alberta, formation of hybrid populations may have occurred gradually during several thousand years. However, the process appears to have stabilized before the region was affected by agricultural disturbances about 100 years ago. I have seen several specimens collected by F.H. Wolley Dod (1901, 1908) around the turn of the century at the "Head of Pine Creek", near Bragg Creek, and these are identical to the hybrid swarm specimens which I have collected in the same area during the last decade.

The Cypress Hills *P. machaon X zelicaon* hybrids are very similar to many of the hybrid specimens from the southern part of the central Alberta hybrid region, and yet do not show any of the more extreme *P. m. hudsonianus*-like characters present in central Alberta. Continuing hybridization with *P. m. dodi* is a possibility in the Cypress Hills, though it would be difficult to demonstrate using the characters employed in this study. However, *P. m. dodi* and *P. zelicaon* appear to hybridize very little in prairie areas of southern Alberta, much like *P. m. oregonius* and *P. zelicaon* in southern British Columbia. Another explanation for the absence of *P. m. hudsonianus*-like specimens may be that the genome of the hybrid swarm is composed of a higher proportion of *P. zelicaon* genes than in central Alberta. Allele distributions in *Pinus contorta* Loudon suggest that the Cypress Hills was a forest refugium during the late Wisconsinan glaciation (Wheeler and Guries, 1982), and so there may have been a *P. machaon* population on the Cypress Hills during this time.

P. polyxenes and hybrids.— *P. p. asterius* has a range approximately as extensive as that of *P. zelicaon* (Figure 43) and shows a similar amount of phenotypic and ecological variation. However, *P. polyxenes* includes several other subspecies and two other species have arisen from the same lineage (Figure 39). The additional *P. polyxenes* subspecies range from the American southwest to northern South America and tend to have a more primitive phenotype expressed in the adults and larvae. They are probably phylogenetically older than the related species in the *P. polyxenes* lineage.

In the *P. polyxenes* lineage is *P. joanae*, which appears to be a taxon with only slight (and dubiously significant) differences from *P. polyxenes*. Also included is *P. brevicauda*, a species restricted to the seashore rim in maritime Canada, which probably survived the late Wisconsinan on the exposed ocean shelves in this region (Figure 41, Matthews, 1979). Adults of both of these species have a wing pattern very similar to *P. p. asterius* and must have achieved reproductive isolation from the latter in the late Pleistocene at the earliest. The gene for the black adult wing morph probably originated in the early Pleistocene, but underwent significant modification during the early history of the *P. polyxenes* lineage, after the divergence of the southern subspecies (Figure 39).

P. p. asterius probably survived the late Wisconsinan in the ecotone between woodland and grassland in the southern part of the eastern and central United States (Figure 41). During post-glacial times this race would have extended its range northward to southern Canada (Figure 43). However, *P. p. asterius* may have had a smaller range and a lower population density before North America was settled by Europeans during the past three centuries (Feeny *et al.*, 1985). It probably reached Nova Scotia only about 60 years ago (Ferguson, 1954), and still seems to be expanding its range in agricultural regions in central Manitoba and Saskatchewan. *P. p. asterius* must have contacted *P. zelicaon* much earlier in the Holocene or even the late Pleistocene, for the black morph on the eastern edge of *P. zelicaon* to have spread several hundred kilometers beyond the range of *P. polyxenes*.

It is doubtful that *P. p. asterius* had any significant amount of contact with *P. m. hudsonianus* during the late Wisconsinan glaciation, even if both survived in refugia within a few hundred kilometers of each other. They are presently allopatric over most of their range, though hybridization has been extensive where they contact each other in central Manitoba. This hybridization shows signs of not yet having reached an equilibrium, since *P. m. hudsonianus* and hybrid forms have become less common in Riding Mountain Park during the past 50 years.

Speciation Mechanisms

Race formation in the *P. machaon* group seems to occur fairly quickly, with ecologically and even phenetically distinctive populations differentiating in a matter of a few thousand years or even a few hundred years under exceptional circumstances. Recent race formation seems to have taken place both at the edge of and in the middle of the range of widespread taxa, when slightly different new larval foodplant resources became available and were opportunistically colonized by individuals from the adjacent population. The most obvious examples include the populations of Californian *P. zelicaon* whose larvae feed on introduced foodplants (Shapiro and Masuda, 1980), and the Peace River race of *P. machaon*

The formation of species seems to have taken much longer than the formation of ecological races, and was probably the result of the adaptation of geographically isolated populations to successively more different habitats. Speciation in the *P. machaon* group probably takes place over hundreds of thousands of years. The low species diversity of the *P. machaon* group in the Palearctic region, despite formation of many geographic races, suggests that speciation can not occur unless there is an extended period of geographic allopatry. However, even if two populations have been separated for enough time to acquire an independent evolutionary identity, hybrid populations may still form between separate species.

The maintenance of separate genetic identity is probably dependent on the degree and kind of ecological differences between two populations when they meet. Genetic mechanisms for

diapause determination are examples of the importance of ecological adaptations in the *P. machaon* group. Hybrids between *P. zelicaon* and *P. machaon* (see phenology section) or *P. polyxenes* (Oliver, 1969) may emerge at a time which is not only different from both of the parental species but is also likely to be inappropriate to the local habitat conditions. Considering the many interrelated factors that are associated with phenology, such as larval foodplant availability, speciation and race formation probably involve substantial reorganization of polygenic balances (*sensu* Carson, 1981).

In the *P. machaon* group, a variety of ecological factors are associated with the coexistence of more than one species in the same geographic region. A difference in larval foodplant is probably the most obvious of these factors. The greatest local species diversity anywhere within the range of the *P. machaon* group occurs in Arizona and southeastern California. Here larvae of *P. indra* feed on umbellifers, those of *P. m. bairdii* feed on composites, and *P. p. coloro* larvae have switched back to a more ancestral foodplant group for *Papilio*, the Rutaceae. However, larval resource partitioning does not necessarily imply competition for these resources (as suggested, for example, by Miller and Brown, 1983). Though Emmel and Emmel (1969) and Blau (1980) have indicated that larval resources may sometimes limit population sizes in the *P. machaon* group, direct larval resource competition between species has not yet been demonstrated.

Natural Hybridization

Hybridization between closely related species is a well known event in both plants and animals. The phenomenon is, by definition, in conflict with the biological species concept. Most animal taxonomists deal with this by describing hybridization as interspecific only if hybrids are rare in comparison with the parental forms. However, for some species pairs, hybridization is relatively common and yet the parental species maintain their integrity. The species in such a taxonomically difficult group are termed semispecies by some authors, while the group itself may be termed a superspecies (Mayr, 1963). The term semispecies is appropriate for the species in the *P. machaon* group, since these are more reproductively isolated than geographic subspecies and yet hybridize relatively freely in comparison to most other species.

Under some conditions, hybrids are especially common. Such conditions include habitat disturbance, of which the most common source is the clearing of forests by man. However, increased rates of hybridization generally take place in very restricted geographic areas. If hybridization occurs along a narrow line of contact between parapatric species, then such an area is referred to as a hybrid zone. Hybrid individuals may comprise small or large proportions of populations in hybrid zones, and may also be present in varying frequencies within larger areas of overlap between parental species. The species of the *P. machaon* group in western Canada show a low but persistent rate of hybridization in most areas where they come into contact, and in some areas have formed populations in which hybrid individuals are numerically dominant (Figure 44).

Hybrid zones.— The zone of hybridization between two species may vary in width from a few hundred meters to more than a hundred kilometers, but is much narrower than the total range of the parental species (Barton and Hewitt, 1981 and 1985). Most hybrid zones are much longer than they are wide, and some span an entire continent. In the *P. machaon* group, the best examples of hybrid zones are along the periphery of the range of *P. polyxenes* In the American West this species replaces *P. zelicaon* along major ecotones. It involves a replacement over a few dozen kilometers of *P. polyxenes* by *P. zelicaon* in wetter habitats and
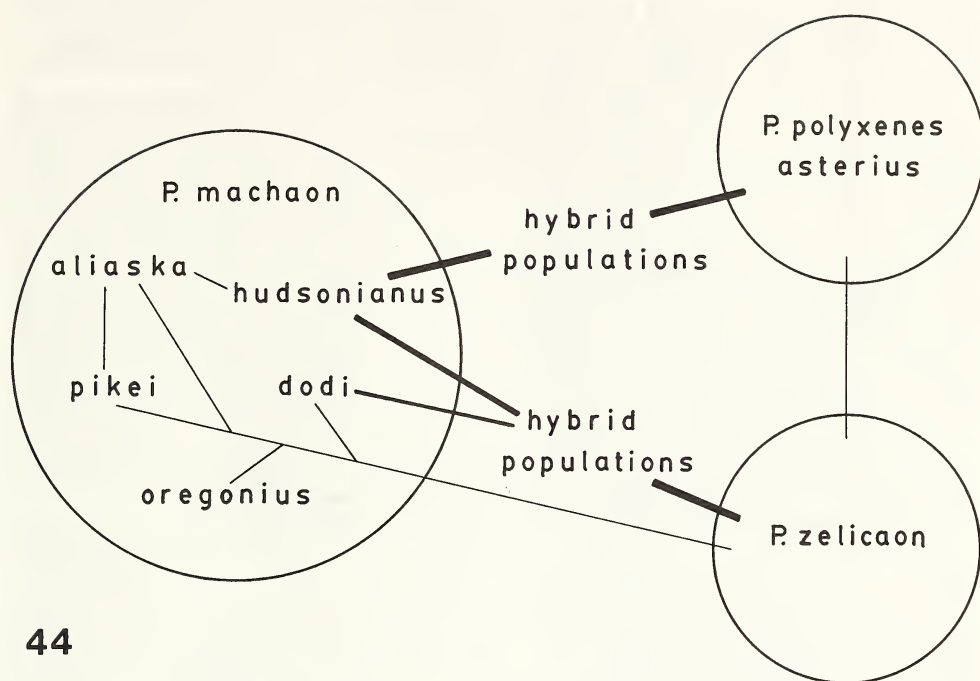
Figure 44. Hybridization of *P. machaon* group species in western Canada during recent time. Circles indicate species. Relative thickness of lines is proportional to rates of hybridization.

higher altitudes. A similar pattern also applies to the transition from *P. polyxenes* to *P. m. hudsonianus* in cooler habitats in Manitoba, though the width of the real zone of intergradation between the two species remains uncertain. In both comparisons, the zones are relatively wide compared to other animals, probably because of the good dispersal powers of *Papilio* butterflies (Shields, 1967).

The pattern of variation across a hybrid zone may not be a simple cline, but rather a mosaic of populations (Harrison, 1986). This is clearly true of the *P. machaon* group, and appears to be closely associated with an interdigitation of habitats across major ecotones.

The influence of environmental factors on the location of major hybrid populations is supported by the coincidence of the *P. zelicaon* X *machaon* populations in central Alberta with ecological boundaries and hybrid zones in other species. For example, the southern limit of the hybrid populations in southern Alberta occurs very near to the southernmost limit of many boreal elements. Black spruce (*Picea mariana* [Mill.]BSP) is found in Alberta only as far south as Bragg Creek, while three butterfly taxa characteristic of spruce bogs are also found south to near Bragg Creek. These include *Colias gigantea gigantea* Strecker, *Oeneis jutta chermocki* Wyatt, and *Erebia disa* (Thunberg). The northern limit of the *P. machaon* X *zelicaon* hybrid populations in central Alberta also coincides generally with the location of several hybrid zones in unrelated taxa. An example is the hybrid zone between *Pinus contorta* and *P. banksiama* Lamb., (with a corresponding contact zone between the pine-feeding butterflies *Incisalia*

eryphon (Boisduval) and *I. niphon* (Huebner), - Reist, 1979). I am not aware of any animal taxa which form self reproducing hybrid populations within Alberta. However, in plants there is a wide ranging hybrid swarm in the genus *Betula*, which has a distribution very similar to that of the *P. machaon X zelicaon* swarms in central Alberta (Dugle, 1966).

Some hybrid zones appear to have moved a few dozen kilometers within the last century (*e.g.,* McDonnell *et al.,* 1978). However, such movement is uncommon, and most hybrid zones appear to remain relatively stationary over long periods of time. In fact, many hybrid zones probably become trapped in regions of low density, such as habitat clines and natural barriers (Barton, 1979). They may also become narrower, especially if there is strong selection against hybrids, or they may widen and eventually result in the merging of the two parental species. In the *P. machaon* group, evidence suggests that some hybrid zones may presently be undergoing change, probably because they are very recent, having been influenced by human settlement patterns. The range expansion of *P. polyxenes* into Nova Scotia and Manitoba is probably related to deforestation by man, and so it seems likely that any interaction of this species with *P. brevicauda*, in the east, and *P. m. hudsonianus*, in the west, is less than a century old. The decreasing proportion of *P. machaon* in Riding Mountain Park in Manitoba is thus probably a result of genetic swamping by recently arrived *P. polyxenes* in agricultural areas.

Most hybrid zones for both plants and animals, appear to be the result of secondary contact between formerly allopatric species (*e.g.,* Remington, 1968b; Barton and Hewitt, 1985). However, a few hybrid zones may be the result of *in situ* differentiation on either end of a sharp environmental gradient (Endler, 1977). Most authors do not believe that they can distinguish between these two situations, though Thorpe (1984) states that a phylogenetic analysis at the population level makes such distinctions possible. In the *P. machaon* group it seems most likely to me that most, if not all, of the hybrid zones can most parsimoniously be explained as the result of post-Pleistocene range expansions. However, if *P. m. hudsonianus* spent the late Wisconsinan south of the continental ice sheet, then there may have been a pattern of contact between *P. m. hudsonianus* and *P. p. asterius* which was similar to the present one. The contact zone between *P. zelicaon* and *P. m. aliaska* is certainly the result of secondary contact.

Hybrid zones which show substantial gene flow are generally no longer considered to represent interspecific hybridization, but rather zones of contact between different races of a single species. Examples include subspecies within both *P. machaon* and *P. polyxenes* in the western United States. However, the degree of gene flow has only been indirectly interpreted from morphological and ecological character gradients and could bear rechecking against enzyme allele distributions. In particular, it should be interesting to compare the rate of gene flow between *P. p. asterius* and *P. p. coloro* in New Mexico with that between *P. p. coloro* and *P. zelicaon* in southern California. Enzyme data for western Canada show a significant interruption in gene flow between *P. machaon* and *P. zelicaon* in most regions in Alberta and British Columbia.

Though both electrophoretic and morphometric character distributions can indicate gene flow across hybrid zones, there may be some differences between these character types. This is true of the *P. machaon* group hybrid populations in both central Alberta and Manitoba, where electrophoretic character combinations showed greater intermediacy than did morphometric characters. Harrison (1986) reported a similar situation in a hybrid zone in crickets, and suggested that there were fewer barriers to the introgression of allozyme alleles than morphometric characters. A possible reason for this is that the inheritance of morphometric characters is more canalized, with a greater degree of linkage between genes and a resultingly

greater resistance to the movement of such traits.

The evolutionary importance of interspecific hybridization is not clear, though various authors have suggested that gene introgression provides an important source of allelic variation for action of natural selection. However, most studies of gene flow in hybrid zones show only limited intrusions of alleles into neighboring species (Barton and Hewitt, 1985). The black morph in the *P. machaon* group generally follows this pattern as well, though it has moved several hundred kilometers into the range of *P. zelicaon* and has displaced the yellow allele in the southern part of the range of *P. machaon*.

The selective advantage of alleles which produce the black adult morph is unknown. Since many populations are polymorphic with respect to this allele, it is probably not important as a visual mechanism for mate recognition, as Hafernik (1982) reported for an analogous wing pattern in *Junonia* (Nymphalidae). It may give hilltopping males an advantage in maintaining a position at the very peak of hills (Scott, 1983 and personal observations). However, Miller (1977) suggested that the allele is lethal when homozygous and in combination with the *P. zelicaon* genome. Perhaps the distribution of the allele is the result of an equilibrium between positive and negative selection, much as hybrid zones themselves may be a balanced conflict between genes that widen zones by reducing incompatibilities and genes that narrow zones by producing reproductive isolation (Barton and Hewitt, 1981).

Hybrid populations.— Some populations in interspecific hybrid zones are characterized by negative or neutral selection on hybrid individuals in the contact zone. However, hybrid populations are characterized by positive selection for interspecific hybrids in restricted areas, even though the parental species retain their integrity over most of their area of contact. Hybrid populations are composed predominantly of hybrid forms, and variation within most such populations spans the full range of phenotypes between the parental forms. In a fully integrated hybrid population, individuals phenotypically similar to parental forms simply represent the phenotypic extremes within the population.

Hybrid populations are reasonably common in plants, with many referred to as hybrid swarms, but are very unusual in animals (Mayr, 1963; Grant, 1971). Most animal examples are of birds, amphibians and fish (Moore, 1977), and the studies of Sibley (1954) on towhees and those of Blair (1941) and others on toads are still among the best documented. Examples of hybrid populations not clearly associated with narrow zones are much less common in insects.

The present study provides a clear example of hybrid populations between broadly sympatric species. In the *P. machaon* group the best examples of hybrid swarms are the *P. machaon X zelicaon* populations in central Alberta, particularly the one at Bragg Creek. The Bragg Creek population is composed of a highly varied but unimodal population made up almost completely of hybrid forms, and probably has no significant internal impediment to gene flow. The intermediate nature of the central Alberta populations is indicated by both the morphometric and electrophoretic character distributions.

Many hybrid populations are associated with environmental disturbance of some sort, resulting in a kind of hybrid habitat, in which forms intermediate between the parental species can flourish. Habitat disturbance by man in recent times, has provided several opportunities to observe the formation of new hybrid swarms over a period of only a few decades (*e.g.,* Gillespie, 1985). An interesting aspect of some hybrid populations is that they separate again into parental forms within about 20 years (Jones, 1973; Corbin *et al.*, 1979). Considering the ephemerality and dependence on habitat disturbance of many hybrid swarms, the examples of the *P. machaon* group from central Alberta are fairly unusual. They occur in areas with

relatively little or no habitat disturbance, especially compared to the regions dominated by agriculture where *P. machaon* and *P. zelicaon* coexist with only a small amount of hybridization. As well, material collected around 1900 suggests that the hybrid populations were already in existence when central Alberta was first being settled.

Although artificial hybrids within the *P. machaon* group have invariably been obtained between individuals from geographically distant populations, and many showed substantial infertility even when they were from interspecific populations clearly connected by character clines, some backcrosses to either of the parental species have produced viable adults (Clarke and , 1953; Ae, 1966; Clarke *et al.*, 1977). In a few crosses, adults have even been obtained from an F_2 hybrid cross of *P. polyxenes* and *P. machaon* (Ae, 1964). These experiments indicate that introgression and the formation of hybrid swarms are at least possible, though unlikely.

However, at least part of the inviability of hybrids is due to environmental adaptations, such as diapause characteristics (Oliver, 1969). Since the three species in western Canada are very flexible in their adaptation to different environmental factors, it is reasonable to expect that species coming together in a particular region tend to be more similar than would populations from more distant regions. Unless some fundamentally different ecological adaptation has occurred, adjacent populations seem likely to meet and hybridize on a continuing basis, until reproductive isolation occurs. Thus the reason for formation of *P. machaon X zelicaon* hybrid swarms in central Alberta is probably related to similarities in the habitat preferences of local races before contact occurred through range expansions. The two species coexist where *P. machaon* larvae feed on *Artemisia* and where adult contact is reduced through the occupation of different habitats. Where *P. machaon* occupies a habitat more similar to that of *P. zelicaon*, as does *P. m. hudsonianus*, the two species have tended to merge, with the hybrid populations feeding on plesiotypically palatable umbellifers. This situation is similar to that described by Mayr (1963) for *Passer domesticus* (Linneaus) and *P. hispaniolensis* Temminck in Europe.

Many plants form hybrid swarms, and the frequency with which such events occur may be related to ecological characteristics of particular taxa (Raven, 1976). Some plant species tend to maximize the saturation density (K) of their populations and are separated by ecological and other extrinsic factors, but have only slightly developed internal barriers to hybridization. They hybridize with related species to form new recombinants, which allow populations to adapt to changing environments. On the other hand, species whose populations maximize their rate of increase (r), such as annual herbs, tend to hybridize much less frequently with each other. Since they are characterized by rapid dipersal and growth in new areas, as well as a high commitment of basic resources to reproduction, barriers to hybridization are much more important to these species. This correspondence between maximization of saturation density and tendency toward hybridization in plants does not seem to apply to the *P. machaon* group. These butterflies would, if anything, be considered as maximizing their rate of increase, since they feed in the larval stage on successional plants and are dependent on rapid colonization and foodplant exploitation. However, it would be interesting to investigate the *P. machaon* group to determine if introgression enhances adaptation to new ecological conditions.

The phylogenetic significance of hybrid swarm formation is uncertain. It may be rare enough in animals so that it has had little influence on evolutionary patterns. However, it may be that such breakdowns in reproductive barriers contribute to the formation of new populations under conditions in which one of the parental species would have been eliminated by habitat destruction. In this way part of the threatened gene pool is saved, albeit in a greatly

altered combination. Formation of hybrid populations may also cause a major disorganization of the polygenic balances of the parental species, leading eventually to speciation through a major new balanced genetic system (Carson, 1981).

New species that may have arisen from interspecific hybrid swarms would be impossible to detect by morphological features if the hybridization occurred between a pair of sibling species. On the other hand, if the new species is the product of hybridization between species A and C, and there exists a species B which is more closely related to A than C is, then the hybrid origin of the new species would be indicated by its discordant character distribution. Unfortunately, as Mayr (1963) pointed out, such a character distribution could also easily be due to the character convergences and parallelisms which one would expect in closely related species with a very similar basic gene pool. For these reasons, the number of animal taxa which have had a hybrid origin has almost certainly been underestimated, and will continue to remain so until there has been ample opportunity to support or reject present taxonomic assignments with independent character suites, such as enzyme alleles or mitochondrial DNA.

ACKNOWLEDGEMENTS

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Appendices: Tables 12-14

Table 12. PCA and DFA loadings for morphometric characters.

Characters	No. of states	Prescaling factor	Morph. char. alone			Morph. + E4 char.			Morph. char. Discr.	
			PC1	PC2	PC3	PC1	PC2	PC3	axis 1	axis 2
1. DHW anal yellow exent	4	0.67	-.088	.127	.277	-.084	.028	.086	-.956	.450
2. DHW eyespot pupil shape	4	0.67	.281	.196	.102	.267	-.058	-.039	2.63	.273
3. DHW anal red/blue separ.	3	1.00	.376	.273	.800	.273	.166	.224	.146	.554
4. Tegula color	3	1.00	.074	-.332	.116	.033	.196	-.154	---	--
5. VFW discal yellow	4	0.67	.515	.064	-.287	.373	.201	.209	.396	.437
6. VFW apical yellow smudge	3	1.00	.088	-.410	.094	.036	.223	-.139	-2.79	1.63
7. VHW postmedian orange	8	0.30	.145	-.286	.164	.089	.199	-.064	.669	-1.10
8. Metathoracic yellow	3	1.00	.367	-.177	-.153	.251	.234	.052	.286	-.459
9. Abdominal ventral line	9	0.25	.562	.152	-.295	.409	.196	.264	-.062	.352
10. Abdominal lateral line	3	1.00	.125	-.488	.099	.059	.267	-.179	.138	1.15
11. Abdominal upper line	9	0.25	-.080	.462	-.141	-.028	-.243	.164	-1.18	3.57
% Variance :			54.6	69.8	78.2	32.2	44.4	52.4	89.9	100.

Table 13.   PCA loadings for electrophoretic characters.

		RF	E4 char. alone			E4 + morph. char.		
			PC1	PC2	PC3	PC1	PC2	PC3
1.	Est4 -A	.48	.513	.153	-.029	-.333	.364	.057
2.	Est4 -B	.54	-.513	-.153	.029	.333	-.364	-.057
3.	Est5 -I	.57	.003	.001	.003	-.001	.002	.004
4.	Est5 -A	.64	.194	-.083	.049	-.134	.028	.202
5.	Est5 -B	.65	.001	.006	-.009	-.001	.005	-.011
6.	Est5 -C	.71	-.188	.080	-.041	.126	-.035	-.197
7.	Est5 -D	.75	-.010	-.004	-.003	.010	.000	.002
8.	IDH -A	.16	.015	.006	.039	-.008	.014	.030
9.	IDH -B	.18	-.178	.109	-.678	.082	-.143	-.490
10.	IDH -C	.20	.012	-.010	.041	-.003	.014	.039
11.	IDH -D	.22	.148	-.108	.595	-.069	.114	.421
12.	IDH -E	.24	.002	.003	.003	-.002	.001	.000
13.	G-6-PD -E	.16	-.006	-.006	-.002	.004	-.006	.001
14.	G-6-PD -A	.18	-.003	-.025	-.046	-.005	-.019	-.028
15.	G-6-PD -B	.20	-.395	-.016	.205	.264	-.232	.001
16.	G-6-PD -I	.22	.027	.026	.023	-.010	.024	.021
17.	G-6-PD -K	.24	-.008	.191	-.017	.036	.168	-.146
18.	G-6-PD -C	.26	.387	-.171	-.206	-.293	.053	.108
19.	G-6-PD -D	.30	.006	.000	.043	.002	.012	.044
20.	ME -J	.475	.001	.017	-.001	.001	.013	-.013
21.	ME -I	.500	.022	.055	-.007	-.016	.026	-.029
22.	ME -A	.525	.110	.076	-.056	-.087	.027	-.028
23.	ME -B	.550	-.118	-.188	.045	.082	-.086	.073
24.	ME -K	.575	-.005	.017	.007	.006	.009	-.006
25.	ME -C	.600	-.010	.015	.013	.012	.005	.007
26.	ME -D	.625	.000	.008	-.002	.001	.006	-.005
27.	ODH -A	.17	-.020	-.020	.001	.014	-.013	.001
28.	ODH -B	.21	.034	.084	.061	-.006	.071	.037
29.	ODH -C	.25	-.014	-.064	-.062	-.008	-.058	-.038
30.	MDH -I	.16	-.004	.008	.001	.003	-.000	-.004
31.	MDH -A	.18	.002	-.013	.014	-.001	-.001	.013
32.	MDH -B	.22	.001	.001	-.024	-.004	-.006	-.014
33.	MDH -C	.26	.002	.004	.008	.001	.007	.004
34.	aGPD -A	.29	-.002	-.001	.000	.001	-.001	.000
35.	aGPD -B	.32	.001	.000	.003	.000	.004	.003
36.	aGPD -C	.35	.000	.001	-.003	-.002	-.002	-.003
37.	Prot1 -A	.21	-.065	.119	.179	.085	.087	.084
38.	Prot1 -B	.26	.065	-.119	-.179	-.085	-.087	-.084
39.	Prot2 -I	.300	.002	.006	.004	-.002	.000	-.001
40.	Prot2 -A	.315	-.042	.613	.067	.073	:278	-.275
41.	Prot2 -B	.330	.037	-.623	-.070	-.070	-.282	.275
42.	Prot2 -C	.345	.003	.004	-.001	-.000	.004	.001
	% Variance :		31.0	43.2	53.0	32.2	44.4	52.4

Table 14. Larval foodplant records.

Only wild collected larvae and confirmed ovipositions under natural conditions are included. Entries are arranged by taxon and region. All entries for a particular locality are grouped together, even though entries from major hybrid zones produced a variety of adults. Uncredited entries refer to personal obsevations or collections. Abbreviations: AB = Alberta, BC = British Columbia, MB = Manitoba, SK = Saskatchewan, NWT = Northwest Territories.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. aliaska				
Pink Mt.(alpine), BC	*Artemisia arctica*	6 July 1981	1 egg	not emg.
Pink Mt.(alpine), BC	*Artemisia arctica*	17 Aug. 1982	4-3rd, 3-4th,16-5th	1m. 2f
Eagle Summit, Alaska	*Artemisia arctica*	1972	1 egg, K.Philip (pers.comm. 1983) not reared	
Dawson, Yukon	*Artemisia arctica*	1949	ovip. obs. by P. Bruggeman (Freeman, 1949)	
Richardson Mts., Yukon	*Artemisia arctica*	June 1981	ovip. obs. by J. Troubridge -*in litt.* 1981. not reared	
near Aklavik, NWT	*Petasites palmatus* var. *frigidus*	1931	larvae observed by O. Bryant (Leussler and Bryant, 1935)	
Arctic Red River, NWT	"small low-growing carroty plant" (?*A. arctica*)	late June 1955	oviposition observed by C. Wyatt (1957)	
P. m. hudsonianus				
Jan Lake, SK	?*Sanicula marilandica*	June 1972	ovip. obs. by G. Anweiler (Hooper, 1973), not reared	
Torch Lake, SK	*Petasites palmatus*	August 1976	1-5th, color photo by G. Anweiler	not reared
P. m. oregonius				
Penticton area, BC	*Artemisia dracunculus*	20 August 1980	6-1st,10-2nd,7-3rd,14-4th,15-5th	1m
Penticton area, BC	*A. dracunculus*	1 July 1984	1-3rd, 1-4th	not reared
Macalister-Soda Cr., BC	*A. dracunculus*	18 August 1982	1-1st,1-3rd,2-4th,16-5th,1 pupa	2m, 2f
Savona, BC	*A. dracunculus*	19 August 1982	1-2nd, 2-5th	2f
Kamloops, BC	*A. dracunculus*	26,27 Aug. 1983	1-e, 2-4th, 15-4th, 56-5th	25m, 23f
Grant Co.Washington	*A. dracunculus*	1 July 1983	"ova & larvae" -Lepidopterists' News (Season Summary 1983)	
Deschutes Park, Oregon	*A. dracunculus*	26 July 1980	14-e,15-1st,25-2nd,12-3rd,6-4th,5-5th	no emg.
Biggs, Oregon	*A. dracunculus*	26 July 1980	1-3rd, 1-4th, 6-5th	1f

(continued on next page)

Table 14 (continued)

P. m. pikei

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
12km ne Hudson Hope, BC	*Artemisia dracunculus*	12 July 1984	2-e, 3-1st	no emg.
12km ne Hudson Hope, BC	*A. dracunculus*	20 August 1984	9-4th, 64-5th	22m, 20f
Attachie, BC	*A. dracunculus*	9 July 1981	2-e,13-1st & 2nd,1-3rd, 1-4th	1m
Attachie, BC	*A. dracunculus*	9 August 1981	11-4th, 41-5th	9m, 4f
Taylor, BC	*A. dracunculus*	18 August 1980	2-5th	1f
Taylor, BC	*A. dracunculus*	8 July 1982	1-2nd, 1-3rd, 1-4th	1m
8 km e. Ft.St.John, BC	*A. dracunculus*	18 August 1980	1-5th	no emg.
Clayhurst Fy., BC	*A. dracunculus*	17 August 1980	1-4th, 59-5th	3m, 5f
Clayhurst Fy., BC	*A. dracunculus*	9 August 1981	3-4th, 46-5th	3m, 2f
Clayhurst Ferry, BC	*A. dracunculus*	16 August 1982	2-4th, 42-5th	12m, 6f
18 mi w Fairview, AB	*A. dracunculus*	21 August 1980	1-5th E.M. Pike -*in litt.*	1980 emg.?
Dunvegan, AB	*A. dracunculus*	13,15,17 Aug.80	4-4th, 24-5th E.M. Pike -*in litt.*	1980 emg.?
Dunvegan, AB	*A. dracunculus*	16 August 1980	6-4th, 32-5th	3m, 3f
Dunvegan, AB	*A. dracunculus*	8 August 1981	7-4th, 15-5th	no emg.
Dunvegan, AB	*A. dracunculus*	15 August 1982	1-4th, 4-5th	1f
10 mi s.w. Fairview, AB	*A. dracunculus*	8 July 1984	1-e, 1-1st (G.J. Hilchie, leg)	no emg.
10 mi s.w. Fairview, AB	*A. dracunculus*	19,28 Aug.& 1 Sept.80	10-5th E.M. Pike -*in litt.*	1980 emg.?
Camp I., s. Whitelaw,AB	*A. dracunculus*	15 August 1982	6-5th	no emg.
Shaftesbury Ferry, AB	*A. dracunculus*	15 August 1980	1-4th	1m
Shaftesbury Ferry, AB	*A. dracunculus*	15 August 1980	2-5th	1f
Peace River (town), AB	*A. dracunculus*	14 August 1980	4-4th, 56-5th	2m, 1f
Peace River (town), AB	*A. dracunculus*	8 August 1981	1-4th, 3-5th	1f
Peace River (town), AB	*A. dracunculus*	24 July 1983	1-2nd	no emg.
12 mi e. North Star, AB	*A. dracunculus*	18 August 1984	11-5th	2m, 1f
Kleskun Hills, AB	*A. dracunculus*	11 August 1981	5-5th	no emg.
Kleskun Hills, AB	*A. dracunculus*	12 August 1981	1-5th	1f

Table 14 (continued)

P. m. dodi

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
Nevis Junction, AB	*Artemisia dracunculus*	19 August 1981	5-5th	1m
Nevis Junction, AB	*A. dracunculus*	3 Sept. 1982	2-3rd, 2-4th, 17-5th	3m, 3f
Nevis Junction, AB	*A. dracunculus*	8 Sept. 1983	2-5th	no emg.
Tolman Bridge, AB	*A. dracunculus*	30 July 1981	4-5th	2m, 1f
Tolman Bridge, AB	*A. dracunculus*	3 Sept. 1982	1-3rd, 4-4th, 20-5th	5m
Morrin Bridge, AB	*A. dracunculus*	2nd wk. July 80	c.50-1st & 2nd J. Troubridge -*in litt*. 1980	emg.?
Morrin Bridge, AB	*A. dracunculus*	10 August 1980	2-2nd, 8-5th	2f
Bleriot Ferry, AB	*A. dracunculus*	2nd wk. July 80	c.50-1st & 2nd J. Troubridge -*in litt*. 1980	emg.?
Bleriot Ferry, AB	*A. dracunculus*	10 August 1980	2-4th, 14-5th	no emg.
Bleriot Ferry, AB	*A. dracunculus*	22 July 1981	2 larvae -4th or 5th	no emg.
Bleriot Ferry, AB	*A. dracunculus*	20 July 1982	1-2nd E.M. Pike, pers. comm.	emg.?
Nacmine, AB	*A. dracunculus*	20 July 1982	2-2nd, 1-3rd, 3-4th, 12-5th E.M. Pike, pers. comm.	emg.?
Nacmine, AB	*A. dracunculus*	2nd wk July 80	c.100-1st & 2nd. J. Troubridge -*in litt*. 1980	emg.?
Nacmine area, AB	*A. dracunculus*	10 August 1980	21-4th & 5th E.M. Pike, pers. comm.	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	c.11 Aug. 1980	40 larvae, mostly 4th & 5th	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	22 July 1981	2-2nd(Bler.); 1-3rd, 4-5th(Nac.)	emg. counted w. Drumheller
Nacmine area(+ Bleriot), AB	*A. dracunculus*	19 August 1981	3-4th, 8-5th	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	19 July 1982	3-4th, 8-5th	emg. counted w. Drumheller
Hwy 575, w. Nacmine, AB	*A. dracunculus*	8 August 1982	5 larvae, ? instars, 1 pupa	no emg.
Drumheller, AB	*A. dracunculus*	22 July 1981	2-2nd, 1-3rd, 3-4th, 12-5th	2m, 3f
Drumheller, AB	*A. dracunculus*	10 August 1980	15 larvae, mostly 4th & 5th	6f
Drumheller, AB	*A. dracunculus*	22 July 1981	3-1st, 3-2nd, 2-3rd, 6-5th	4m, 5f
Drumheller, AB	*A. dracunculus*	19 July 1982	2-4th, 17-5th	1m, 2f
Drumheller area, AB	*A. dracunculus*	8 August 1982	1-4th, 7-5th E.M. Pike, pers. comm.	emg.?
Drumheller, AB	*A. dracunculus*	20 July 1982	1-4th, 4-5th	no emg.
East Coulee, AB	*A. dracunculus*	3 Sept. 1982	250 larvae, mostly 1st & 2nd E.M. Pike, pers. comm.	no emg.
East Coulee, AB	*A. dracunculus*	2nd wk July 80	7-1st, 5-2nd, 8-3rd, 8-4th, 7-5th J. Troubridge -*in litt*. 1980	no emg.
East Coulee, AB	*A. dracunculus*	10 August 1980	3-larvae, 4th or 5th	no emg.
East Coulee, AB	*A. dracunculus*	19 August 1981	3-4th, 1-5th	no emg.
East Coulee, AB	*A. dracunculus*	19 August 1981	3-4th, 1-5th	no emg.
Dorothy, AB	*A. dracunculus*	2nd wk July 80	48 larvae, mostly 1st & 2nd J. Troubridge -*in litt*. 1980	no emg.
Dorothy, AB	*A. dracunculus*	10 August 1980	1-e, 1-1st, 1-2nd, 3-3rd, 1-4th, 3-5th	2m, 1f
Dorothy, AB	*A. dracunculus*	19 July 1982	5-2nd, 1-3rd, 2-5th	1f
Dorothy, AB	*A. dracunculus*	8 August 1982	1-4th	no emg.

Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. dodi - continued				
Outlook, SK	*A. dracunculus*	9 Sept. 1982	1-2nd, 1-3rd, 1-4th, 10-5th	6m, 1f
Outlook, SK	*A. dracunculus*	28 May 1983	ovip. observed	not reared
Calgary, AB	*A. dracunculus*	30 August 1983	2-4th	no emg.
Spring Coulee, AB	*A. dracunculus*	29 August 1983	3-4th, 4-5th	4f
Taber Prov. Park, AB	*A. dracunculus*	10 August 1980	1-1st E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	7 August 1980	50 larvae, 2nd to 5th E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	9 August 1980	40 larvae, 2nd to 5th E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	26 August 1980	13-4th, 37-5th	7m, 17f
8 mi. s. Vauxhall, AB	*A. dracunculus*	29 July 1981	c.100 larvae, mostly 1st & 2nd	no emg.
8 mi. s. Vauxhall, AB	*A. dracunculus*	19 August 1981	c.70 larvae, mostly 4th & 5th	17m, 10f
8 mi. s. Vauxhall, AB	*A. dracunculus*	6 July 1982	30 larvae, mostly 5th E.M. Pike, pers. comm.	4m, 3f
8 mi. s. Vauxhall, AB	*A. dracunculus*	8 July 1982	10 larvae, 4th or 5th E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	29 August 1983	1-2nd, 1-3rd, 7-4th, 13-5th	6m, 3f
P. m. bairdii				
Canyonlands NP, Utah (Needles District)	*Artemisia dracunculus*	20 May 1985	2-3rd	not reared

Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. zelicaon				
southern & interior BC				
Saanich, BC	*Lomatium nudicale*	1957		G.A. Hardy-leg. specm. in BCPM 1f + 1?m C. Guppy -*in litt.* 1982
Francis Peak, BC	*Oenanthe sarmentosa*	8 August 1962		G.A. Hardy-leg. specm. in BCPM 1f R. Guppy (1970)
Ucluelet, BC	*Heracleum lanatum*	May & July	2nds to 5ths both months	
Thetis Island, BC	"garden parsley"	"often"	?instars	"a major foodplant" -H. Kimmich *in litt.* 1982
Abbotsford, BC	*Angelica lucida*	?date	?instars	
Abbotsford, BC	*Sium suave*	end of Aug. 82	mostly 5ths	Kimmich *in litt.* 1982 in FAHS colln: 3m,7f
Abbotsford, BC	*Angelica genuflexa*	end of Aug. 82	mostly 5ths	Kimmich *in litt.* 1982 included above
Abbotsford, BC	*O. sarmentosa*	c. 10 Aug. 1984	?instars	Kimmich *in litt.* 1984 in FAHS colln: 7m,9f
Abbotsford, BC	*Cicuta occidentalis*	c.10 Aug. 1984	?instars	Kimmich *in litt.* 1984 included above
Matsqui, BC	*Sium suave*	July & August	all instars	Kimmich *in litt.* 1982 ?emg.
Manning Park, BC	*Osmorhiza chilensis*	? date	?instars	Kimmich *in litt.* 1982 ?emg.
Kootenay Skyway Smt.,BC	*Heracleum lanatum*	20 August 1982	1-3rd	1f
5 km s Enderby, BC	*Heracleum lanatum*	30 June 1984	6-2nd, 2-3rd	incl. w. next entry
5 km s Enderby, BC	*Heracleum lanatum*	2 July 1984	3-2nd, 7-3rd, 1-4th, 7-5th	4m, 1f
11 km w Revelstoke, BC	*Heracleum lanatum*	30 June 1984	1-1st, 4-2nd	3m
Rogers, BC (Glacier NP)	*Heracleum lanatum*	30 June 1984	1-1st, 2-2nd	no emg.
Tete Jaune Cache, BC	*Heracleum lanatum*	26 August 1983	1-5th	no emg.
Barkerville, BC	*Heracleum lanatum*	August	?instar	N. Criddle-leg, McDunnough (1927) 1f
Macleod Lake,n PrGeo.BC	*Zizia aptera*	? date	?instars	?emg.
Bear Lk.n.Prince Geo.BC	*Heracleum lanatum*	18 August 1982	1-5th	H. Kimmich *in litt.* 1982 1-5th
Peace River region				
Pink Mt. (valley), BC	*Heracleum lanatum*	16 & 17 Aug. 82	5-4th, 3-5th	no emg.
Pink Mt. (valley), BC	*Heracleum lanatum*	19 August 1984	1-3rd, 1-5th	no emg.
10km ne Hudson Hope, BC	*Heracleum lanatum*	12 July 1984	5-1st, 2-2nd, 3-3rd, 1-4th	3m
15 km w Ft.St. John, BC	*Heracleum lanatum*	12 July 1984	6-1st,9-2nd,4-3rd,2-4th,2-5th	no emg.
Cecil Lake, BC	*Heracleum lanatum*	9 July 1984	4-1st, 2-2nd	E.M. Pike -pers. comm. ?emg.
30 ml w Dawson Creek,BC	*Zizia aptera*	2 July 1982	1-2nd, 1-3rd, 1-4th	1m, 1f
30 ml w Dawson Creek,BC	*Zizia aptera*	10 July 1984	2-1st	no emg.
40 km w Dawson Creek,BC	*Heracleum lanatum*	10 July 1984	2-1st, 6-2nd, 1-3rd	no emg.
18 km w Dawson Creek,BC	*Heracleum lanatum*	10 July 1984	17-1st, 6-2nd, 3-3rd, 3-5th	1m
w. Chetwynd, BC	*Heracleum lanatum*	18 August 1982	1-5th	no emg.
Thunder Mt., BC	*Heracleum lanatum* & *Angelica genuflexa*	9 July 1982	7-1st, 9-2nd, 4-3rd	1m

Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. zelicaon - continued				
14 mi. w. Elmworth, AB	Heracleum lanatum	9 July 1982	2-1st, 4-2nd	not reared
3.5 km nw Wembley, AB	Heracleum lanatum	10 July 1984	4-1st, 5-2nd, 3-3rd, 2-4th	1m, 3f
3.0 km nw Wembley, AB	Sium suave	10 July 1984	1-e, 4-1st	1m
2 km e Woking, AB	Heracleum lanatum	8 July 1984	1-1st, 5-2nd, 2-3rd	1f
2 km e Woking, AB	Zizia aptera	8 July 1984	2-1st	no emg.
2 km w Debolt, AB	Sium suave	12 July 1984	1-5th	1f
13 mi. w Valleyview,AB	Heracleum lanatum	9 July 1982	5-2nd, 8-3rd, 18-4th, 22-5th	2m, 1f
13 mi. w Valleyviw, AB	Heracleum lanatum	12 July 1984	8-1st,17-2nd,8-3rd,4-4th,6-5th	no emg.
15 mi e High Prairie,AB	Heracleum lanatum	27 July 1983	2-3rd	1f
11 mi. s. Dixonville,AB	Heracleum lanatum	27 July 1983	1-3rd	not emg.
Twin Lks.(n.Manning),AB	Heracleum lanatum	25 July 1983	4-5th, 2-4th	2m
southern Alberta & Saskatchewan				
Coleman area, AB	Angelica dawsoni	27 July 1981	3-e, 2-1st, 3-2nd	no emg.
Coleman area, AB	Angelica dawsoni	18 August 1981	1-1st, 2-3rd, 1-5th	no emg.
Coleman area, AB	Angelica arguta	18 August 1981	1-2nd, 7-3rd, 6-4th, 8-5th	no emg.
9 mi se Beaver Mines,AB	Angelica arguta	19 August 1981	1-4th	no emg.
9 mi se Beaver Mines,AB	Angelica dawsoni	21 August 1982	1-3rd	no emg.
9 mi se Beaver Mines,AB	Heracleum lanatum	21 August 1982	1-5th	no emg.
Waterton Park, AB	Angelica arguta	27 July 1981	35 larvae, 1st & 2nd instar	no emg.
Waterton Park, AB	Angelica arguta	19 August 1981	c.100 larvae, mostly 5th	6m, 8f
Waterton Park, AB	Angelica dawsoni	19 August 1981	1-5th	1m
Waterton Park, AB	Lomatium dissectum	19 August 1981	6+ larvae, 4th & 5th	2m, 3f
Waterton Park, AB	Heracleum lanatum	19 August 1981	1-5th	no emg.
Waterton Park, AB	Angelica arguta	21 August 1982	5-2nd, 5-3rd, 3-4th, 4-5th	1f
Waterton Park, AB	Angelica dawsoni	21 August 1982	1-3rd	no emg.
Waterton Park, AB	Lomatium triternatum	21 August 1982	1-4th	no emg.
Waterton Park, AB	Heracleum lanatum	21 August 1982	3-5th	2f
Waterton Park, AB	Angelica arguta	29 August 1983	1-2nd, 4-4th, 15-5th	3f
Waterton Park, AB	Heracleum lanatum	29 August 1983	1-5th	no emg.
Eston, Sask.	"garden dill"	September 1955	larvae prod. both yel. & bl. adults - Hooper (1973:65)	
western US				
Gothic, Colorado	Angelica ampla	2-3 Aug. 1980	1-1st, 2-3rd, 16-4th, 18-5th	1f

Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. machaon X *zelicaon* - Hybrid zone, Umbellifers				
northern region				
Faust, AB	*Heracleum lanatum*	5 July 1984	3-2nd, 3-3rd	2m
22 km e Slave Lake	*Heracleum lanatum*	5 July 1984	5-1st, 2-2nd, 2-3rd	1m, 1f
Fox Creek, AB	*Heracleum lanatum*	10 July 1982	1-1st, 3-2nd, 9-3rd, 7-4th	not reared
Fox Creek, AB	*Heracleum lanatum*	14 August 1982	2-4th, 2-5th	1f
Fox Creek, AB	*Angelica genuflexa*	14 August 1982	1-5th	not emg.
30 km e Fox Creek, AB	*Heracleum lanatum*	13 July 1984	3-1st, 6-2nd, 1-4th	no emg.
7 mi. s. Whitecourt, AB	*Heracleum lanatum*	10 July 1982	1-5th	no emg.
Cherhill, AB	*Heracleum lanatum*	10 July 1982	1-5th	no emg.
Ft. Saskatchewan, AB	garden celery	9 August 1984	1-5th	1m
Rock Lake, AB	*Heracleum lanatum*	29 August 1982	4-5th (A. Nimmo, leg.)	1f
3 mi n Moberly Lkt.. AB	*Heracleum lanatum*	13 July 1982	2-1st, 3-2nd	no emg.
Switzer Park, AB	*Zizia aptera*	5 July 1980	2-e, 2-2nd, 1-3rd, 1-4th	2m
Switzer Park, AB	*Zizia aptera*	17 July 1981	2-e, 1-2nd	not emg.
Switzer Park, AB	*Zizia aptera*	13 July 1982	1-2nd	not emg.
Switzer Park, AB	*Heracleum lanatum*	13 July 1982	8-1st, 2-2nd	no emg.
Switzer Park, AB	*Heracleum lanatum*	2 Aug. 1982	38-1st & 2nd,2-3rd,2-4th,1-5th: no emg., Pike -pers. comm.	
central region				
3 mi. sw. Thorsby, AB	*Heracleum lanatum*	15 July 1982	1-5th	included with Buck Lk.
e. of Buck Lk.. AB	*Heracleum.lanatum*	16 July 1982	2-2nd, 5-3rd, 6-4th, 27-5th	5m, 5f
Rimbey, AB	*Heracleum lanatum*	16 July 1982	2-4th	1f
7 mi. w. Sylvan Lk..AB	*Heracleum lanatum*	16 July 1982	1-3rd	1f
19 mi. e. Nordegg, AB	*Heracleum lanatum*	17 July 1982	11-1st, 10-2nd. 1-3rd	4m
2 mi. s. Nordegg, AB	*Heracleum lanatum*	17 July 1982	1-1st	no emg.
4 mi e Elm Cr. Cpgd..AB	*Zizia aptera*	17 July 1982	1-2nd	
10 mi e Limestone Mt.AB	*Heracleum lanatum*	17 July	1-3rd	
Didsbury, AB	"parsnip"	? ? 1908	produced 1 m (form *nitra*), in Canadian National Collection	
Waiparous Cpgd.. AB	*Zizia aptera*	20 July 1981	4-2nd	no emg.
southern region				
3 mi se. Bragg Creek,AB	*Zizia aptera*	12 & 14 July 80	8 larvae, 1st & 2nd	no emg.
3 mi se. Bragg Creek,AB	*Zizia aptera*	18 July 1982	1-3rd	no emg.
3 mi se. Bragg Creek,AB	*Zizia aptera*	18July- 7Aug.82	11-1st, 20-2nd, 6-3rd, 4-4th	11m, 13f
Chain Lks. Prov. Pk..AB	?*Angelica arguta*	18 July 1982	2-3rd E.M. Pike - pers. comm.	not reared

Table 14 (continued)

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. polyxenes X *machaon*	- Hybrid Zone			
Somme, SK	"parsnip"	Sept. 1977	? instars	D. Hooper leg. & colln. 1m
Weekes, SK	"parsnip"	Sept. 1977	? instars	D. Hooper leg., SMNH colln. 1m, 2f
Fort Qu'Appelle, SK	"carrot"	c. 1977	one larva	R. Hooper leg.(pers. comm.) not emg.
Gypsumville, MB	*Zizia aptera*	1982	? instar	P. Klassen leg. & colln. 1m
Duck Mt. Prov. Park,MB	*Zizia aptera*	23 June 1980	1-2nd, 1-3rd	FAHS leg. & colln. 1f
Duck Mt. Prov. Park,MB	*Zizia aptera*	reared 1982	? instars	J. Troubridge leg. 3m,5f in FAHS colln.
Riding Mt. Nat. Pk.,MB	*Zizia aptera*	18-25 June 1955	"several hundred eggs and newly hatched larvae" -Remington (1956)	
	- foodplant determined in Heron & Robinson (1976)			
Riding Mt. Nat. Pk.,MB	"wild parsnip" & "meadow parsnip"	2 July 1978	? instars	P. Klassen leg. & colln. 2m,1f
Riding Mt. Nat. Pk.,MB	*Zizia aptera*	21-22 June 1980	11-2nd & 3rds, 1-4th	no emg.
Rid. Mt. Park area, MB	*Zizia aptera*	1982	?inst. (prod. 40 pupae)	H. Kimmich leg. & colln. ?emg.
Rid. Mt. Park area, MB	*Zizia aptera*	19 July 1977	? instars	J. Troubridge leg. & colln. ?emg.
Clan William, MB	"parsnip"	Sept. 1970	? instars	R. Hooper colln. 1m,1f
Gladstone, MB	*Zizia aptera*	20 June 1983	4-1st & 2nds	P. Klassen leg.,FAHS colln. 1m,1f
Culross, MB	"parsley"	23 July 1977	"mature larva"	P. Klassen leg. & colln. 1m
Culross, MB	*Zizia aptera*	30 June 1982	? instar	P. Klassen leg. & colln. 1f

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Quaestiones

Entomologicae

CONTENTS

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ABSTRACT

The 22 species of the Anthonomus *subgenus* Anthomorphus *Weise are hypothesized to constitute a monophyletic group on the basis of morphological characters of the adult weevils. Other adult morphological characters are cited as evidence in proposing a hypothesis of phylogenetic relationships among the species. The species of* Anthomorphus *occur in the Nearctic, Palearctic and Neotropical faunal realms and are known to have hosts in the plant families Pinaceae, Rosaceae, Malpighiaceae, and possibly Betulaceae. A diagnosis and description of the subgenus and of each of the species in the subgenus, a key, and illustrations are presented as aids in identifying the species. Thirteen new species are described:* A. rosadonetoi *(Brazil);* A. howdenorum *(Venezuela);* A. rulfoi *(México);* A. bechyneorum *(Brazil, Honduras, Venezuela);* A. stockwelli *(Panamá);* A. diamantinaensis *(Brazil);* A. camoiranensis *(Venezuela);* A. vanini *(Brazil);* A. bordoni *(México, Venezuela);* A. haliki *(Brazil);* A. chinculticensis *(México);* A. pimentai *Argentina; Bolivia, Brazil)* and A. galphimiae *(México). Lectotypes are designated for* A. paraguayanus *Hustache and* A. sulcipygus *Champion.*

RESUMÉN

Carácteres morfológicos de los adultos indican que las 22 especies de Anthonomus *del subgénero* Anthomorphus *constituyen un grupo monofilético. Se citan otros rasgos morfológicos de los adultos como evidencia de una hipótesis de las relaciónes filogenéticas entre las especies. Las especies de* Anthomorphus *se encuentran en las Regiones Paleártica, Neártica y Neotrópica y tienen plantas hospederas en las familias Pinaceae, Rosaceae, Malpighiaceae, y posiblemente Betulaceae. Se presentan carácteres diagnósticas y una descripción del subgénero y de cada especie del subgénero, además de una clave, y ilustraciónes para auxiliar en la identificación de las especies. Se describen trece especies nuevas y se designan lectotipos para dos especies previamente descritas (véase el resumen en inglés).*

INTRODUCTION

The *Anthonomus* subgenus *Anthomorphus* Weise contains 22 species that occur in the Nearctic, Palearctic and Neotropical faunal realms. The species have been collected in association with plants in several families, including Betulaceae, Fagaceae, Malpighiaceae, Myricaceae, Rosaceae and Pinaceae. Of these, only Malpighiaceae, Rosaceae and Pinaceae have been established by rearing as actual hosts. Some of the species have been collected on Malpighiaceae in association with species of *Anthonomus* in the *venustus* and *unipustulatus* groups (Clark, 1987; Clark and Burke, 1985) and members of the anthonomine genus *Pseudanthonomus*. The present study was undertaken to provide descriptions or redescriptions, illustrations, and a key to facilitate identification of the species. The information on these species is currently being analyzed to determine their relationships to the *Anthonomus*

venustus and *unipustulatus* groups, the genus *Pseudanthonomus* Dietz and other Anthonominae known or suspected to have hosts in the Malpighiaceae.

MATERIALS AND METHODS

Specimens of 653 adults, including types of most of the previously described species, were examined. These were from collections of the following institutions (abbreviations in parentheses are used to refer to collections in the text): Auburn University Entomological Collections (AUEM), Auburn, W.E. Clark; Museu Paraense Emilio Goeldi (MPEG), Belém, W.L. Overal; Museum of Comparative Zoology (MCZC), Cambridge, S. R. Shaw; Illinois Natural History Survey (INHS), Champaign, J. K. Bouseman; Field Museum of Natural History (FMNH), Chicago, J.S. Ashe; Texas A&M University (TAMU), College Station, H.R. Burke; Universidade Federal do Paraná (DZUP), Curitiba, G. Rosado-Neto; Deutsches Entomologisches Institut (IPZE), Eberswalde, L. Dieckmann; Cornell University (CUIC), Ithaca, J.K. Liebherr; Snow Entomological Museum, University of Kansas (SEMC), Lawrence, P.A. Ashlock; The British Museum (Natural History) (BMNH), London, R.T. Thompson; Universidad Central de Venezuela (IZAV), Maracay, L.J. Joly; The American Museum of Natural History (AMNH), New York, L.H. Herman, Jr.; Canadian National Collection of Insects and Arachnids (CNCI), Ottawa, D.E. Bright; Muséum National d'Histoire Naturelle (MNHP), Paris, H. Perrin; Carnegie Museum of Natural History (ICCM), Pittsburg, J.E. Rawlins; California Academy of Sciences (CASC), San Francisco, D.H. Kavanaugh; Museu de Zoologia (MZSP), Universidade de São Paulo, U. Martins; Centre National de Recherches Agronomiques (LFEV), Versailles, J. d'Aguilar; National Museum of Natural History (USNM), Washington, D.C., D.R. Whitehead; Purdue University (PURC), West Lafayette, A.V. Provonsha. The following provided specimens from their personal collections: C. Bordón (CCBM), Maracay; H.A. Hespenheide (CHAH), Los Angeles; H. and A. Howden (HAHC), Ottawa; M.A. Ivie (CMIV), Columbus; C.W. O'Brien (CWOB), Tallahassee; E.L. Sleeper (ELSC), Long Beach.

Measurements were made with the aid of an ocular micrometer in a dissecting microscope as follows: total length from anterior margin of eyes to elytral apices in lateral view; width across elytra at widest point; length of pronotum from anterior to posterior margins; length of rostrum from anteroventral margin of eye to tip, across arc, in lateral view; length of distal portion of rostrum from antennal insertions to tip in lateral view; width of frons at narrowest point between eyes; width of base of rostrum just distad of eyes in dorsal view; and width of pro- and metafemora in anterior view excluding the ventral teeth. The range and, in parentheses, the mean and sample size of each measurement is given for each species.

Relationships of the species of *Anthomorphus* to each other were analyzed using PAUP, Phylogenetic Analysis Using Parsimony, Version 2.4, developed by Swofford (1985), on an IBM Personal Computer (see Phylogeny section).

Subgenus *Anthomorphus* Weise

Anthomorphus Weise 1883: 255. *Type species* (by subsequent designation: Dieckmann 1968: 470): *Curculio varians* Paykull.

Paranthonomus Dietz 1891: 199. *Type species* (by original designation): *Anthonomus profundus* Le Conte.

Recognition.— The species of *Anthonomus* in the subgenus *Anthomorphus* are distinguished by the following combination of characters:

1) abdomen of male (Fig. 37) with sternum 5 subquadrately emarginate, leaving triangular, setose sclerite isolated from posterior margin (except in *A. pinivorax*);

2) pygidium of male (Figs. 33–36) and of female (Figs. 38–46) sulcate or impressed (except in *A. diamantinaensis* and female *A. rosadonetoi*).

Description.— Male. *Length*: 1.8–4.1 mm. *Width*: 1.0–2.0 mm. *Head*: vertex with median fovea, sparsely, minutely punctate, with narrow, setiform scales; venter with slightly to much broader, more pallid scales, eyes round, posterior margin slightly elevated so that greatest convexity occurs there. *Rostrum*: length 1.0–1.8 x pronotal length; in dorsal view, sides converging slightly from base to antennal insertions, subparallel or gradually diverging from there to tip; proximal portion rugose-punctate to distinctly carinate; dorsal margin of lateral rostral groove carinate, directed to middle of eye; distal portion shallowly punctate to rugose-punctate, length 16–39% of total rostral length; antennal funiculus with 7 articles. *Thorax*: sides evenly rounded from subapical constriction; evenly convex from constriction to base; pronotum densely, coarsely punctate, each puncture giving rise to a narrow scale; broader scales whitish, limited to dorsal midline and to lateral portions, narrower scales aeneous, forming broad lateromedian vittae; pleuron with punctation and vestiture as on pronotum, scales on lower portions slightly broader and more pallid. *Elytra*: humeri not prominent, sides subparallel in basal 1/2; striae deep, punctures slightly impinging on interspaces; interspaces more-or-less uniformly convex, sutural interspaces narrow at extreme base, these and interspaces 2–5 slightly widened and slightly elevated posterior to shallow obliquely transverse depression; each interspace with median row of narrow to setiform scales and lateral rows of slightly broader scales directed toward center of interspace. *Abdomen*: sternum 5 about as long as sternum 4; each sternum with large, platelike, internal apodeme. *Legs*: apices of femora truncate, narrowly emarginate; profemur slightly stouter than metafemur, with large ventral tooth and in some species a smaller, more distal tooth; metafemur with one small acute ventral tooth; protibia straight to slightly, broadly concave medially on dorsal margin, ventral margin with more-or-less abruptly delimited median prominence, with or without preapical tooth, apically uncinate; metatibia more nearly straight than protibia, slightly widened or narrowed at apex.

Female. *Length*: 2.0–4.2 mm. *Width*: 1.0–2.1 mm. *Rostrum*: length 1.2–2.3 x pronotal length; broadly, evenly curved; length of distal portion 25–49% of total rostral length. *Pygidium*: with or without dorsomedian impression or sulcus.

Discussion.— The subgenus *Anthomorphus* was established by Weise (1883: 255) to include *Anthonomus varians* (Paykull) and *A. perforator* (Herbst), along with *A. ater* (Marsham), cited as a synonym of the latter. Weise stated that the subgenus was characterized by the "*unguiculi dentati*" (toothed tarsal claws) of the included species. Dieckmann (1968: 471) noted that this characterization was in error and that, in fact, *A. varians* is the species with untoothed tarsal claws (the "*unguiculi mutici*" of Weise). Dieckmann (1968: 474) listed *A. perforator* as a "Farbaberration" (color variety) of *A. varians* and noted that *A. ater* is a junior synonym of *A. rubi* (Herbst). He listed *A. varians* as type species of the subgenus *Anthomorphus*, noting that that species, like the type species of the subgenus *Paranthonomus* Dietz, has "ein gefurchtes Pygidium." On the basis of this pygidial character, Dieckmann (1968) also included the Palearctic *A. pinivorax* Silfverberg [as *A. pubescens* (Paykull)]. He listed the name *Anthomorphus* as a synonym of *Paranthonomus*, but did not explain why he used the name *Paranthonomus* for the taxon instead of the older name, *Anthomorphus*.

The name *Paranthonomus* was proposed by Dietz (1891) for a subgenus of *Anthonomus* including the North American *Anthonomus profundus* LeConte, *A. rubidus* LeConte and *A. vulpinus* Dietz, all of which were characterized as having a "deep, longitudinal excavation of the pygidium." Dietz (1891: 200) also stated that in Europe *Paranthonomus* is "represented by *A. pubescens*, and probably *A. pyrenaeus*." (The latter name is also a "Farbaberration" of *A. varians*, according to Dieckmann [1968: 474]).

Champion (1903) considered his *sulcipygus* group, including the Panamanian *A. sulcipygus* Champion, to be the same as Dietz's *Paranthonomus*. Schenkling and Marshall (1934) listed *A. sulcipygus* and 18 additional Neotropical species as members of the subgenus. With the exception of *A. abdominalis* Champion, these species do not have the diagnostic characters of *Anthomorphus* and they are not retained in the subgenus. The relationships of these other species have not been satisfactorily determined, although some have been included in recently completed revisionary studies. For example, *A. melanostictus* and *A. venustus* were assigned to

the *venustus* group by Clark and Burke (1985), and *A. cossonoides* was assigned (as a synonym of *A. instabilis* Faust) to the *gularis* group by Clark and Burke (1986a).

Burke (1962: 205–206) placed *A. unipustulatus* in *Paranthonomus*, citing the sulcate pygidium but noting that in that species the sulcus is "shorter and less deeply excavated" than in *A. profundus* and *A. rubidus*. The association of the Peruvian *A. sulcatus* Kirsch and *A. filicornis* Hustache from Guadeloupe with *Anthomorphus* was not made before the types were examined in connection with the present study. O'Brien and Wibmer (1982:105) and Wibmer and O'Brien (1986: 203) listed *Paranthonomus* as a subgenus of *Anthonomus* but did not indicate which species belong to the group.

The following species are included in the subgenus *Anthomorphus*.

Anthonomus rubidus species group
    Anthonomus rubidus LeConte
    Anthonomus bordoni new species
    Anthonomus paraguayanus Hustache
    Anthonomus profundus LeConte
        Anthonomus vulpinus Dietz
    Anthonomus galphimiae, new species
    Anthonomus howdenorum, new species
    Anthonomus varians (Paykull)
    Anthonomus pinivorax Silfverberg
Anthonomus sulcatus species group
    Anthonomus sulcipygus Champion
    Anthonomus chinculticensis, new species
    Anthonomus vanini, new species
    Anthonomus camoiranensis, new species
    Anthonomus stockwelli, new species
    Anthonomus filicornis Hustache
    Anthonomus sulcatus Kirsch
    Anthonomus pimentai, new species
    Anthonomus bechyneorum, new species
    Anthonomus haliki, new species
    Anthonomus rulfoi, new species
    Anthonomus abdominalis Champion
    Anthonomus diamantinaensis, new species
    Anthonomus rosadonetoi, new species

Males of the species of *Anthomorphus* are distinguished by the characters in the following key. With some exceptions, noted in the treatments of the appropriate species, females are morphologically uniform throughout the subgenus. This presented problems in determining the identity of some species previously described from females only. Furthermore, several females remain among the specimens examined that cannot confidently be associated with identified males or females. Even though non-genitalic characters are preferentially used in the key, the male genitalia provide the best diagnostic characters.

Key to Species of *Anthomorphus* (males only)

1   Abdominal sternum 5 subquadrately emarginate, with triangular, setose sclerite isolated from posterior margin (Fig. 37) 2

1′   Abdominal sternum 5 not subquadrately emarginate, with triangular, setose sclerite isolated from posterior margin ....
.... *A. pinivorax* Silfverberg, p. 330

2 (1)   Tasral claws simple, without basal tooth ..... *A. varians* (Paykull), p. 329

2′   Tarsal claws toothed 3

3 (2′)   Pygidium sulcate (Figs. 33–36) 4

3′   Pygidium not sulcate .... *A. diamantinaensis,* new species, p. 340

4 (3)   Metasternum with long, fine, erect, setiform scales 5

4′   Metasternum with scales (somewhat setiform and slightly raised in some, but not erect) 9

5 (4)   Meso- and metafemora with sparse ventral fringe of long, fine, setiform scales 6

5′   Meso- and metafemora without ventral fringe of setiform scales 8

6 (5)   Metatibia with ventral fringe of long, setiform scales ....
.... *A. rulfoi,* new species, p. 339

6′   Metatibia without ventral fringe of setiform scales 7

7 (6′)   Profemur with large tooth distal to ventral tooth; pronotum and elytra with fine aenescent scales; aedeagus as in Fig. 48 ....
.... *A. bordoni,* new species, p. 325

7′   Profemur with small or obsolescent distal tooth; pronotum and elytra with fine whitish scales; median lobe of male genitalia as in Fig. 47 ....
.... *A. rubidus* LeConte, p. 323

8 (5′)   Metatibial uncus with apical prominence; pygidial sulcus broad, not delimited apically .... *A. galphimiae,* new species, p. 328

8′   Metatibial uncus without apical prominence; pygidial sulcus narrower, delimited apically .... *A. howdenorum,* new species, p. 328

9 (4′)   Profemur with distal tooth distinctly separated from large ventral tooth 10

9′   Profemur without distal tooth, or with slight indication of distal tooth arising from basal portion of ventral tooth 17

10 (9)   Metatibia with ventral fringe of long, aenescent, setiform scales in distal 1/2 .... *A. camoiranensis,* new species, p. 332

10′   Metatibia without ventral fringe of setiform scales 11

11 (10′) Elytra with dark discal macula (indistinct and limited to sutural interspaces in *A. haliki*); strial punctures large, elytral vestiture fasciculate 12

11′   Elytra without dark discal macula; strial punctures smaller, elytral vestiture not fasciculate 13

12 (11) Vestiture of prothorax broad scales and strongly differentiated setiform scales; meso- and metafemora without ventral fringe of long, fine setiform scales .... *A. bechyneorum,* new species, p. 337

12′   Vestiture of prothorax elongate, narrow, acuminate scales; meso- and metafemora with ventral fringe of long, fine, setiform scales ....
.... *A. haliki,* new species, p. 338

ANTHONOMUS RUBIDUS SPECIES GROUP

Recognition.— The members of the *rubidus* species group are distinguished by the following combination of characters:

1) spiculum gastrale of male genitalia with basal portion closely engaging sides of aedeagus, with ventral keel (Fig. 69) (except in *A. pinivorax*);

2) aedeagus with midventral, subbasal lobe (Figs. 47–53) (except in *A. pinivorax*, Fig. 54).

Discussion.— This group includes the two North American, two Palearctic, and five Neotropical species. Three monophyletic subgroups are also recognized. One includes *A. rubidus*, *A. bordoni* and *A. paraguayanus*, all of which have the apical portion of the aedeagus somewhat asymmetrical (Figs. 47–49). Another includes *A. profundus*, *A. howdenorum* and *A. galphimiae*. These have the sutural interspaces slightly to markedly expanded subapically. The last subgroup includes the Palearctic *A. varians* and *A. pinivorax*, distinguished from the New World species by several characters, including possession of sparse, whitish, setiform scales on the elytra. As indicated above, one of these, *A. pinivorax*, lacks the diagnostic characters of the *rubidus* group. It is assigned to the group on the basis of other characters it shares with *A. varians* which indicate that the two are sister species.

Host relationships of the North American species in the *rubidus* group have not been determined with certainty, but the most likely hosts are in the plant family Rosaceae and possibly Betulaceae. Hosts of four of the five Neotropical species are unknown, but at least one is associated with Malpighiaceae. The Palearctic species are unusual among anthonomines in having hosts in the family Pinaceae.

Anthonomus rubidus LeConte

Anthonomus rubidus LeConte, 1876: 199. Hamilton 1885: 106. Dietz 1891: 200–201. Fall 1913: 47. Blatchley and Leng 1916: 291. Burke 1962: 206. *Holotype*: Pennsylvania, male [Penn.] [Type 1959] [J.L. Leconte/Coll.] [A. rubidus/*Lec*.] (MCZC).

Recognition (Fig. 1).— This North American species is distinguished by the following combination of characters:

1) mesosternum, abdominal sterna, and meso- and metafemora of male with long, sparse, setiform scales;
2) elytra with midbasal macula extended posteriorly on suture (Fig. 2);
3) aedeagus slightly asymmetrical (Fig. 47);
4) endophallus with sparse, minute proximal denticles, with larger, irregular median denticles (Fig. 47).

It closely resembles *A. bordoni* from Venezuela from which it is distinguished by the smaller, less distinct distal profemoral tooth, the longer, more dense, erect, setiform scales on the metasterum, abdomen, and metafemur and by slight differences in the male genitalia (Figs. 47, 48). It is most likely to be confused with the North American *A. profundus* from which it is distinguished by the following characters:

1) vestiture of pronotum and elytra denser (Figs. 1, 2, 5, 6);
2) sutural elytral interspaces without subapical prominences (Fig. 5);
3) pygidial sulcus narrower in male and female (Figs. 33, 38, 39);
4) long setiform scales on male metasternum and meso- and metafemora;
5) aedeagus less strongly asymmetrical (Figs. 47, 50);
6) profemora less strongly inflated, with more well-developed distal tooth;
7) and, protibia without preapical tooth.

As noted by Hamilton (1885: 106), specimens of *A. rubidus* have been confused in collections with those of *Pseudanthonomus crataegi* Walsh. However, as Hamilton noted, "there should not be much trouble in distinguishing (the two species), as *crataegi* has only six joints in the funicle of the antenna, while *rubidus* has seven – a matter readily determined by counting them under a microscope."

Description.— Male. *Length*: 2.1–2.6 mm ($\bar{x}=2.4$, n=15). *Width*: 0.9–1.3 mm ($\bar{x}=1.2$, n=15). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: slender, length 1.1–1.5 x ($\bar{x}=1.3$, n=15) pronotal length; broadly, evenly curved; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion finely, sparsely punctate, length 21–28% ($\bar{x}=25$, n=15) of total rostral length. *Thorax*: pronotum with dark, narrow aenescent scales and with middorsal vitta of long, narrow, pallid whitish scales. *Pygidium*: median sulcus wider and deeper toward apex. *Legs*: profemur slender, ca. 1.3 x stouter than metafemur, with distal tooth that shares common base with larger ventral tooth in some specimens; protibia without preapical tooth; metatibial uncus long, straight, oblique, truncate.

Female. *Length*: 2.2–2.6 mm ($\bar{x}=2.4$, n=15). *Width*: 1.1–1.3 mm ($\bar{x}=1.2$, n=15). *Rostrum*: length 1.2–1.4 x ($\bar{x}=1.2$, n=15) pronotal length; broadly, evenly curved; proximal portion rugose, vestiture limited to proximal 1/3; distal portion smooth, length 27–35% ($\bar{x}=30$, n=15) of total rostral length. *Pygidium* (Fig. 38): with broadly rounded apicodorsal prominence; median sulcus long, straight to slightly wider posteriorly, with long, dense setae. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Plant Associations.— Label data indicate that specimens of *A. rubidus* have been collected on the following plants:

Betulaceae

    Betula lutea Michx. (under surface of leaves, 1 specimen, McKeever, Herkimer Co., New York)

    Corylus (20 specimens, Kappa, Illinois; 2 specimens, Haddon Heights, New Jersey)

Fagaceae

    Quercus alba (1 specimen, Westerville, Ohio)

Juglandaceae

    wild hickory (1 specimen, Tippecanoe Co., Indiana)

Rosaceae

    "cherry" (4 specimens, Tippecanoe Co., Indiana)

    Prunus demissa D. Dietr. (1 specimen, Bountiful, Davis Co., Utah)

    Prunus serotina J.F. Ehrh. (1 specimen, Albemarle Co., Virginia, 2 specimens, Rhea Co., Tennessee)

    "wild cherry" (1 specimen, Tippecanoe Co., Indiana).

Distribution.— This species is widespread in North America from Canada to Florida, westward to Minnesota and Illinois, with an extralimital record in Utah. In addition to the holotype of *A. rubidus* from Pennsylvania, specimens from the following localities were examined.

CANADA. *Québec.* Aylmer (1 female, ICCM). Duparquet (1 female, USNM).

UNITED STATES. *Connecticut.* New Haven Co.: Wallingford (1 female, CWOB). *District of Columbia.* Kennelworth Pond (1 female, TAMU). *Florida.* Duval Co. (1 female, USNM). *Georgia.* White Co.: Helen (2 males, USNM). *Illinois.* (1 female, FMNH; 1 female, ICCM). Woodford Co.: Kappa (4 males, 3 females, TAMU, 8 males, 5 females, USNM). *Indiana.* Tippecanoe Co. (1 female, TAMU, 12 males, 3 females, USNM). *Iowa.* (1 male, USNM). *Kentucky.* Fayette Co.: (1 male, USNM). *Maryland.* Garrett Co.: Deer Park (1 female, USNM). Prince Georges Co.: Beltsville (1 female, USNM) (1 female, USNM); Bladensburg (1 female, USNM). Washington Co.: Boonsboro (1 male, 3 females, TAMU). *Massachusetts.* (1 male, SEMC). Adams Co.: Mt. Greylock (1 female, CUIC). Barnstable Co.: East Sandwich (1 female, USNM). Natick Co.: Sherborn (1 male, MCZC). *Michigan.* Marquette Co.: Marquette (1 female, USNM). Midland Co.: (1 female, USNM). Muskegon Co.: Henry (1 female, USNM). *Minnesota.* Rice Co.: Nerstrand Woods (1 female, CWOB). *New Hampshire.* Coos Co.: Carter Dome, White Mountains (4 males, USNM); Carter Notch, White Mountains (3 females, USNM). Grafton Co.: Franconia (1 male, AMNH). *New Jersey.* Camden Co.: Haddon Heights (1 male, 1 female, CNCI). Monmouth Co.: Hornerstown (1 male, AMNH). Morris Co.: Budd Lake (1 male, AMNH). *New York.* Herkimer Co.: McKeever (1 female, USNM). Ulster Co.: Slide Mt. (14 males, 1 female, USNM) (2 males, 1 female, USNM). *North Carolina.* Yancey Co.: Black Mountains (1 male, 1 female, AMNH, 1 female, CASC). *Ohio.* (1 male, SEMC). Franklin Co.: Westerville (1 female, ELSC). Hamilton Co.: Cincinnati (1 male, USNM). Hocking Co.: 8 mi. SW Logan, S.R. 664 (1 female, CMIV). *Pennsylvania.* Allegheny Co.: Pittsburg (2 males, 2 females, ICCM). Forest Co.: 1 mi E Neiltown (1 female, USNM). Indiana Co.: Indiana (1 male, AMNH). Northampton Co.: Wind Gap (1 male, CASC). Westmorland Co.: Jeannette, 15, 20, 28 (1 male, CNCI; 3 males, 1 female, ICCM). York Co.: 5 mi. N Davidsburg (1 female, USNM). *Tennessee.* (1 female, USNM). Davidson Co.: Nashville (1 female, USNM). Great Smoky Mountain National Park (2 males, 1 female, HAHC). Rhea Co.: (2 males, USNM) (1 male, 1 female, USNM). Sevier Co.: Gatlinburg (1 male, 1 female, USNM). *Utah.* Davis Co.: Bountiful (1 male, USNM). *Virginia.* Albemarle Co.: (2 males, 1 female, USNM), (1 male, USNM). Alexandria Co.: (1 male, USNM). Washington Co.:

Blacksburg (1 male, USNM). *West Virginia.* Fort Pendleton (1 female, USNM). The specimens were collected in the months of May-October.

Anthonomus bordoni, new species

Type Series.— *Holotype*: Venezuela, male [VENEZUELA: Merida/Jaji/25 June 1983/W.E. Clark and Clark] [Host 83V–09] (USNM). *Paratypes*: México, 1 male [MEXICO, N.L. 2200 m. El/Potosi Mt. 8 km. NW, 18/de Marzo Galeana Aug. 26, 1977 A. Garcia A.] [on pine/& oak]. Venezuela, 4 males, 6 females [VENEZUELA: Merida/Jaji/26 June 1983/W.E. Clark and Clark -] [Host 83V–09]; 1 male [Venezuela AR/Rancho Grande/1100 m 17–VIII–1965] [F. Fernando-Y./J. Salcedo/Cols.] [A La Luz]; 1 female [La Grita m./2300. TACHIRA] [VENEZ. Bordón/leg. 25 III 1985]. Total paratypes, 13 (AUEM, CCBM, CWOB, IZAV, TAMU).

Recognition (Fig. 3).— This species is distinguished by the following combination of characters:

> 1) metasternum, abdominal sterna, and meso- and metafemora with sparse ventral fringe of long setiform scales;
>
> 2) aedeagus asymmetrical (Fig. 48);
>
> 3) elytra with midbasal macula extended posteriorly on suture (Fig. 4);
>
> 4) endophallus with minute proximal denticles, with sparse median denticles and large median tooth (Fig. 48).

It resembles the North American *A. rubidus* from which it is distinguished by the more distinct distal tooth on the profemur and, in the male, by the longer, more dense setiform scales on the metasternum, abdomen, and metafemur. The aedeagus also differs slightly in the two species (Figs. 47, 48).

Description.— Male. *Length*: 2.4–2.8 mm ($\bar{x}=2.6$, n=6). *Width*: 1.1–1.4 mm ($\bar{x}=1.3$, n=6). *Head*: eyes separated by distance ca. 0.7 x width of rostrum at base. *Rostrum*: slender, length 1.0–1.5 x ($\bar{x}=1.4$, n=6) pronotal length; broadly, evenly curved; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion finely, sparsely punctate, length 19–30% ($\bar{x}=26$, n=6) of total rostral length. *Thorax*: pronotum with elongate, narrow, dark fulvo-aeneous scales and middorsal vitta of broader, more pallid scales. *Pygidium*: median sulcus broad anteriorly, deeper and slightly wider posteriorly, not extended to apex. *Legs*: profemur narrow, ca. 1.3 x stouter than metafemur; distal tooth small, acute; protibia with acute preapical tooth; metatibial uncus minute, slightly hooked.

Female. *Length*: 2.6–2.9 mm ($\bar{x}=2.7$, n=8). *Width*: 1.2–1.4 mm ($\bar{x}=1.4$, n=8). *Rostrum*: length 1.4–1.6 x ($\bar{x}=1.5$, n=8) pronotal length; broadly, evenly curved; proximal portion rugose, vestiture limited to extreme base; distal portion smooth, length 29–36% ($\bar{x}=34$, n=8) of total rostral length. *Pygidium*: broadly rounded apically; median sulcus long, narrow, shallow, not wide posteriorly, without setae. *Abdomen*: sterum 5 with posterior margin nearly straight.

Plant Associations.— The type series of *A. bordoni* was taken on an unidentified tree.

Distribution.— This species is known only from the type series from Venezuela and México.

Specific Epithet.— This species is named in Honor of Carlos Bordón of Maracay, Venezuela, as a token of appreciation for his friendship and assistance.

Anthonomus paraguayanus Hustache

Anthonomus paraguayanus Hustache 1939: 55–56. *Lectotype* (here designated): Paraguay, male [Paraguay/Hohenau] [(♀)] ·[TYPE] [MUSEUM PARIS/1949/Col. A. Hustache] [Anthonomus/paraguayanus/m.] (MNHP). *Paralectotypes*: Paraguay, 1 male [Paraguay/Hohenau] [Syntypus] [Anthonomus/paraguayanus/co-type m.] [Coll. DEI/Eberswalde] (IPZE); 1 female [Paraguay/Hohenau] [(♀)] [TYPE] [MUSEUM PARIS/1949/Col. A. Hustache] (MNHP). Hustache (1939: 55–56) indicated that this species was described from four females, but the IPZE "co-type" and one of two MNHP syntypes examined are males.

Recognition.— This species is distinguished by the following combination of characters:

> 1) metasternum, abdominal sterna, and meso- and metafemora of male without long setiform scales;
>
> 2) aedeagus asymmetrical, constricted to narrowly rounded apex (Fig. 49);
>
> 3) metatibial uncus with prominence;

4) elytra with midbasal macula extended posteriorly on suture;

5) endophallus with sparse proximal denticles and a large distal tooth (Fig. 49).

It closely resembles the North American *A. rubidus* and *A. bordoni* from Venezuela. It is distinguished from these two species by the absence of long setiform scales on the male femora, the distinct prominence on the male metatibial uncus, and by differences in the male genitalia (Figs. 47–49).

Description.— Male. *Length*: 1.8–2.5 mm ($\bar{x}$=2.2, n=6). *Width*: 1.0–1.1 mm ($\bar{x}$=1.0, n=6). *Head*: eyes separated by distance ca. 0.8 x width of rostrum at base. *Rostrum*: slender, length 1.0–1.5 x ($\bar{x}$=1.3, n=6) pronotal length; broadly, evenly curved; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion finely, sparsely punctate, length 27–35% ($\bar{x}$=32, n=6) of total rostral length. *Thorax*: pronotum with long, narrow aenaescent scales and middorsal vitta of broader, more pallid fulvous scales. *Pygidium*: median sulcus narrow posteriorly, wider and deeper apically. *Legs*: profemur slender, ca. 1.4 x stouter than metafemur, with minute distal tooth that shares common base with larger ventral tooth; protibia without preapical tooth.

Female. *Length*: 2.1–2.4 mm ($\bar{x}$=2.2, n=2). *Width*: 1.0 mm ($\bar{x}$=1.0, n=2). *Rostrum*: short, length 1.5 x ($\bar{x}$=1.5, n=2) pronotal length; slightly, evenly curved; proximal portion smooth, vestiture limited to extreme base; distal portion smooth, length 34–35% ($\bar{x}$=35, n=2) of total rostral length. *Pygidium*: broadly rounded, apicodorsal prominence obsolete; median sulcus short, shallow, remote from apex, not wider apically. *Abdomen*: sternum 5 with posterior margin slightly concave medially.

Plant Associations.— Unknown.

Distribution.— *Anthonomus paraguayanus* is known only from northern Argentina and southern Brazil. In addition to the lectotype and paralectotypes from Paraguay, the following specimens were examined.

ARGENTINA. *Misiones*. El Dorado (1 female, AMNH).

BRAZIL. *Santa Catarina*: Nova Teutônia (5 males, 1 female, ELSC, HAHC, MZSP). The specimens were collected in August, September and November.

Anthonomus profundus LeConte

Anthonomus profundus LeConte 1876: 198. Schwarz 1890: 232. Hamilton 1895: 376. Pierce 1907: 268. Fall 1913: 46–47. Leng 1920: 322. Schenkling and Marshall 1934: 38. Burke 1962: 206. Hatch 1971: 349–350. *Lectotype* (designated by Burke (1984: 265): Illinois, female [(small golden disc)] [Type/1958] [J.L. LeConte/coll.] [LECTOTYPE/Anthonomus/profundus/LeC./design. by/H.R. Burke] [A. profundus/*Lec.*] (MCZC).

Anthonomus vulpinus Dietz 1891: 201. *Lectotype* (designated by Burke 1984: 262–263): Pennsylvania, male [Pa.] [Type/1955] [W.G. Dietz/Coll.] [LECTOTYPE/Anthonomus/vulpinus/Dietz/design. by/H.R. Burke] (MCZC). This synonymy was recognized by Fall (1913: 46–47) who stated that "... the differences given by Dietz... do not look as important in the specimens themselves as they appear on paper," as well as by Leng (1920: 322), Schenkling and Marshall (1934: 38), and O'Brien and Wibmer (1982: 109).

Anthonomus profundus vulpinus Dietz: Blatchley and Leng 1916: 291

Recognition (Fig. 5).— This species is distinguished by the following combination of characters:

1) metasternum and abdominal sterna, and meso- and metafemora without long setiform scales;

2) metafemora of male stout, strongly curved, the single small ventral tooth displaced distally;

3) metatibia of male straight, without midventral prominence;

4) sutural elytral interspaces with subapical prominences that are widely separated in female (Fig. 39);

5) aedeagus strongly curved in distal 1/3 (Fig. 50);

6) pygidial sulcus of male broad, slightly narrowed posteriorly, delimited apically (Fig. 33);

7) elytra with midbasal macula extended posteriorly on suture;

8) endophallus with sparse, minute denticles and a large sclerotized plate (Fig. 50).

It resembles the Mexican *A. galphimiae* from which it is distinguished by the characters listed in the section on that species. It is likely to be confused with the North American *A. rubidus* but the two are distinguished by the characters listed in the section on the latter.

Description.— Male. *Length*: 2.8–4.1 mm (x̄=3.3, n=11). *Width*: 1.2–2.0 mm (x̄=1.5, n=11). *Head*: eyes separated by distance ca. 0.7 x width of rostrum at base. *Rostrum*: length 1.3–1.5 x (x̄=1.4, n=11) pronotal length; most strongly curved over antennal insertions; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion shallowly rugulose-punctate, length 16-25% (x̄=21, n=11) of total rostral length. *Thorax*: pronotum with elongate, acuminate, aeneous setiform scales and middorsal vitta of broader whitish scales. *Legs*: profemur ca. 1.4 x stouter than metafemur, distal tooth obsolete or absent; protibia with small, acute preapical tooth; metatibial uncus short, curved, excavated.

Female. *Length*: 2.5–3.7 mm (x̄=3.1, n=9). *Width*: 1.2–1.7 mm (x̄=1.5, n=9). *Rostrum*: slender, short, length 1.3–1.6 x (x̄=1.5, n=9) pronotal length, most strongly curved over antennal insertions; proximal portion rugose, vestiture limited to extreme base; distal portion smooth, length 28–37% (x̄=31, n=9) of total rostral length. *Pygidium* (Fig. 39): with strongly rounded apicodorsal prominence; median sulcus long, broad, slightly wider apically. *Abdomen*: sternum 5 with posterior margin straight.

Plant Associations.— According to Pierce (1907: 268) "Mr. Schwarz states that this species breeds in *Crataegus* buds." Schwarz (1890: 232) himself, however, stated that the species "develops within the fruit of *Crataegus crus-galli*, the imago appearing in July." Label data indicate that specimens of *A. profundus* have been collected on the following plants (the *Larix* record is probably an incidental association):

Rosaceae
  Amelanchier canadensis (L.) Medic. (4 specimens, Beltsville, Maryland)
  Aronia arbutifolia (L.) Ell. (1 specimen, Beltsville, Maryland)
  Aronia "purpuria" (2 specimens, Pemberton, Burlington Co., New Jersey)
  Crataegus sp. (2 specimens, Westerville, Franklin Co., Ohio)
Pinaceae
  Larix laricina (Du Roi) K. Koch (1 specimen, Volo, Lake Co., Illinois)

Distribution.— This species occurs in eastern Canada and the northeastern United States, westward to Illinois and southward to Texas, and in California and Oregon. The specimens from McMinnville, Oregon, referred to by Hatch (1971: 350), were not examined. In addition to the lectotype of *A. profundus*, which LeConte (1876: 198) stated was from Illinois, and the lectotype of *A. vulpinus* from Pennsylvania, the following specimens were examined.

CANADA. *Nova Scotia.* Dartmouth (1 male, USNM). *Ontario.* Mer Bleue (1 male, 1 female, CNCI); Port Credit (1 female, USNM); Toronto (1 female, USNM).

UNITED STATES. *California.* Trinity Co.: Carrville (1 male, 1 female, CASC). *Illinois.* Lake Co.: Volo (1 female, INHS). *Indiana.* Crawford Co.: (1 female, USNM). Marshall Co.: (1 male, PURC); Starke Co.: (1 male, PURC). *Iowa.* Johnson Co.: Iowa City (1 male, 1 female, USNM). *Maryland.* Garrett Co.: Oakland (4 males, 5 females, USNM). Prince Georges Co.: Beltsville (1 male, CNCI) (1 female, USNM) (2 males, 2 females, USNM) (1 male, 1 female, USNM); Priest Bridge (1 male, USNM). *Massachusetts.* (2 males, 2 females, USNM). Berkshire Co.: North Adams (1 female, USNM). Hampden Co.: Springfield (1 male, USNM) 1 female, USNM). Middlesex Co.: Ashland (1 female, CASC); Framingham (1 male, 3 females, USNM) (1 male, USNM); Natick (1 male, 1 female, CASC); Sherborn (1 female, CASC); Wilmington (1 female, USNM). Plymouth Co.: Marion (1 male, USNM). *Michigan.* Eaton Co.: Grand Ledge (1 female, USNM). Ingham Co.: 2 mi. SW Holt (2 males, TAMU). Ottawa Co.: 1 mi. S. Grand Haven (1 male, 1 female, TAMU). *New Jersey.* Bergen Co.: Ramsey (2 males, USNM). Burlington Co.: Browns Mills (1 male, 1 female, CNCI); Pemberton (2 females, USNM). Essex Co.: Caldwell (1 male, 1 female, USNM); Montclair (1 female, USNM); Newark (1 male, 1 female, USNM). Gloucester Co.: Malaga (2 males, 1 female, USNM) (1 female, USNM); Midwood (1 male, AMNH). Ocean Co.: Lakehurst (7 males, 5 females, USNM). Union Co.: Berkeley Heights (1 female, USNM); Elizabeth, 27 Nov (1 female, USNM). *New York.* New York City (1 male, 6 females, USNM). Nassau Co.: Massapequa (2 males, 1 female, USNM). St. Lawrence Co.: Cranberry Lake (1 female, USNM). *Ohio.* Franklin Co.: Westerville (1 male, 1 female, ELSC). Hamilton Co.: Cincinnati (1 female, USNM). *Oregon* (1 male, 2 females, USNM). *Pennsylvania* (4 females, USNM). Clearfield Co.: Clearfield (2 females, USNM). Fayette Co.: Oliver (2 females, USNM). Lycoming Co.: North Mount (1 female, USNM). Monroe Co.: Canadensis (2 females, USNM). *Texas.* (1 male, INHS). *West*

Virginia. Greenbriar Co.: White Sulphur Spring (2 males, USNM). Marion Co.: Fairmont (1 female, CASC). Pocahantas Co.: Cranberry Glades (1 male, CMIV). The Specimens were collected in the months of April-August.

Anthonomus galphimiae, new species

Type Series.— *Holotype*: México, male [MEXICO: Chiapas/ 27 km SE Teopisca/ 22 Sept. 1981/ Clark and Coe] [collected on/*Galphimia*/ *glauca* Cav., det./W.R. Anderson, 1981] (USNM). *Paratypes*: México, 4 males, 3 females [MEXICO: Chiapas/27 Km SE Teopisca/ 22 Sept. 1981/ Clark and Coe] [collected on/ *Galphimia*/ *glauca* Cav., det./ W.R. Anderson 1981]; 1 male [MEXICO. Oax. Hwy 175/ 10 Km NE Oaxaca/ 1800 m 16.VI.1979/ H & A Howden]. Total paratypes, 8 (AUEM, HAHC, TAMU).

Recognition (Figs. 7).— This species is distinguished by the following combination of characters:

> 1) metasternum and abdominal sterna, but not meso- and metafemora, with long, fine erect, aeneous, setiform scales;
>
> 2) pygidial sulcus of male broad, not narrowed posteriorly, not delimited apically;
>
> 3) pygidial sulcus of female broad, deep, wider apically (Fig. 40);
>
> 4) aedeagus symmetrical, expanded apically (Fig. 51);
>
> 5) elytra with midbasal macula extended posteriorly on suture (Fig. 8);
>
> 6) endophallus with sparse, minute proximal denticles, a small distal field of denticles, a small toothlike sclerite and lightly sclerotized tube (Fig. 51).

It resembles *A. profundus* in having the pygidial sulcus of the male and female unusually broad and deep (Figs. 33, 39, 40), but is distinguished from that species by the coarser vestiture, less strongly inflated, less strongly curved femora that have larger ventral teeth which are not displaced distally, and by the shape of the aedeagus (Figs. 50, 51).

Description.— Male. *Length*: 3.2–3.5 mm ($\bar{x}$=3.4, n=6). *Width*: 1.5–1.7 mm ($\bar{x}$=1.6, n=6). *Head*: eyes separated by distance ca. 0.8 x width of rostrum at base. *Rostrum*: length 1.4–1.5 x ($\bar{x}$=1.4, n=6) pronotal length; broadly, evenly curved; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion shallowly rugulose-punctate, length 19–23% ($\bar{x}$=22, n=6) of total rostral length. *Thorax*: pronotum with elongate, acuminate, ferruginous scales and middorsal vitta of broader whitish scales. *Legs*: profemur ca. 1.1 x stouter than metafemur, with small, acute distal tooth; protibia with short, acute preapical tooth; metatibial uncus large, with basal prominence.

Female. *Female*: 3.2–3.3 mm ($\bar{x}$=3.3, n=3). *Width*: 1.6–1.7 mm ($\bar{x}$=1.6, n=3). *Rostum*: length 1.4–1.5 x ($\bar{x}$=1.5, n=3) pronotal length; broadly, evenly curved; proximal portion rugose, vestiture limited to proximal 1/3; distal portion smooth, length 37–39% ($\bar{x}$=38, n=3) of total rostral length. *Pygidium* (Fig. 40): with broad, apicodorsal prominence; medium sulcus delimited by narrow carina, with long, dense, setae. *Abdomen*: sternum 5 with posterior margin slightly produced, with slight apicolateral prominences.

Plant Associations.— The type series was collected on Malpighiaceae (*Galphimia glauca* Cav.).

Distribution.— This species is known only from the type series from México.

Specific Epithet.— The name of this species is an anagram of the generic name of its host.

Anthonomus howdenorum, new species

Type Series.— *Holotype*: Venezuela, male [VENEZUELA: Tach.: 3300m. 55 km. NE/ San Cristobal/ V.17–18.1974/ H. & W. Howden] (HAHC). *Paratypes*: Venezuela, 1 male, 1 female [VENEZUELA: H. & A. Howden]; 1 male [VENEZUELA: Tachira/ Pueblo Hondo/ 28 June 1983/ W.E. Clark and Clark]; 1 female [Páramo la Negra/ Venezuela, Táchi-/ ra m./ 24–VI–1979] [B. Bechyne/ leg.]. Total paratypes, 4 (AUEM, HAHC, IZAV).

Recognition (Fig. 9).— This species is distinguished by the following combination of characters:

> 1) metasternum and abdominal sterna, but not meso- and metafemora, with long, fine, erect, setiform scales;
>
> 2) elytra with subfasciculate white, fulvous and fuscous scales;

3) sutural elytral interspaces slightly expanded subapically;

4) aedeagus (Fig. 52) strongly asymmetrical;

5) endophallus with minute proximal denticles and a large toothlike sclerite (Fig. 52);

6) elytra with midbasal macula extended posteriorly on suture (Fig. 10).

The aedeagus of this species is similar in form to that of *A. profundus* (Figs. 50, 52). The distinctive pattern of strongly differentiated, subfasciculate, white, fulvous and fuscous elytral scales is unique among known *Anthomorphus*.

Description.— Male. *Length*: 2.8–3.1 (x̄=2.9, n=3). *Width*: 1.2–1.4 mm (x̄=1.3, n=3). *Head*: eyes separated by distance ca. 0.8 x width of rostrum at base. *Rostrum*: length 1.4–1.5 x (x̄=1.4, n=3) pronotal length; most strongly curved over antenna insertions; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion shallowly rugulose-punctate, length 20–22% (x̄=21, n=3) of total rostral length. *Thorax*: pronotum with elongate, acuminate ferruginous scales and middorsal vitta of broader whitish scales. *Pygidium*: median sulcus narrow, wider and deeper apically. *Legs*: profemur ca. 1.3 x stouter than metafemur, with small distal tooth; protibia with large, acute preapical tooth; metatibial uncus slender, straight, oblique.

Female. *Length*: 3.0–3.2 mm (x̄=3.1, n=2). *Width*: 1.4–1.5 mm (x̄=1.4, n=2). *Rostrum*: stout, length 1.5 x (x̄=1.5, n=2) pronotal length; slightly, evenly curved; proximal portion sulcate, vestiture extensive almost to antennal insertions; distal portion smooth, length 31–32% (x̄=32, n=2) of total rostral length. *Pygidium*: with strongly rounded apicodorsal prominence; median sulcus narrow, deep, not wider apically, with long, dense setae. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Plant Associations.— Unknown.

Distribution.— This species is known only from the type series from Venezuela.

Specific Epithet.— This species is named in honor of Henry and Ann Howden of Ottawa, Ontario, Canada, in appreciation of their friendship and encouragement.

Anthonomus varians (Paykull)

Curculio varians Paykull 1792: 16. *Type Material*: Sweden, not examined, lost (Diechmann 1968: 473).
Anthonomus varians (Paykull). Dieckmann 1968: 473–478 (synonyms listed).

Recognition (Figs. 11, 12).— This species is distinguished by the following combination of characters:

1) elytra with sparse setiform scales;

2) eyes small, round, prominent;

3) femora strongly inflated;

4) rostrum slender, smooth, glabrous from base to tip;

5) tarsal claws simple, without basal tooth;

6) ventral margin of metatibia of male curved;

7) aedeagus symmetrical, narrowed distally (Fig. 53);

8) endophallus unarmed (Fig. 53).

It is distinguished from the other Palearctic species of *Anthomorphus*, *A. pinivorax*, by the curved male metatibia (Dieckmann, 1968: Fig. 38), the unarmed tarsal claws and the asymmetrical, distally narrowed aedeagus (Fig. 53). It resembles *A. pinivorax* in several characters by which the two Palearctic species are distinguished from their New World relatives. These are the sparse setiform elytral scales, the small round, prominent eyes, the strongly inflated femora, the slender, smooth, glabrous rostrum and the unarmed endophallus of the male genitalia.

Description.— (see Dieckmann, 1968: 475).

Plant Associations.— Dieckmann (1968: 475–477) reported that *A. varians* occurs on *Pinus sylvestris* L., *P. montana* Mill., and occasionally on *Picea abies* L. Dieckmann also cited various authors who stated that the larvae develop in the buds of the young shoots or in the cones, and according to his own observations, in the male inflorescences.

Distribution.— According to Dieckmann (1968: 477) *A. varians* is widespread throughout Europe, the Near East, and central and eastern Siberia.

Anthonomus pinivorax Silfverberg

Anthonomus pinivorax Silfverberg 1977: 14. Replacement name for *Curculio pubescens* Paykull 1792: 12 (not Fabricius 1775: 131). Dieckmann 1968: 478–479 (lists synonyms). *Lectotype*: Sweden (designated by Dieckmann 1968: 478), not examined.

Recognition.— This species is distinguished by the following combination of characters:
1) elytra with sparse setiform scales;
2) eyes small, round, prominent;
3) femur strongly inflated;
4) rostrum slender, smooth, glabrous from base to tip;
5) tarsal claws with basal tooth;
6) metatibia of male straight;
7) aedeagus symmetrical, widened distally (Fig. 54);
8) endophallus unarmed (Fig. 54);
9) abdomen of male with sternum 5 not subquadrately emarginate, without triangular, setose sclerite isolated from posterior margin (Fig. 37).

It is distinguished from the other Palearctic species of *Anthomorphus, A. varians*, by the straight male metatibia (Dieckmann, 1968: Fig. 39), the symmetrical aedeagus that is widened distally (Fig. 54), and the toothed tarsal claws.

Description.— (see Dieckmann, 1968: 478–479).

Plant Associations.— Dieckmann (1968: 479) reported that *A. pubescens* occurs on *Picea abies* L., *Pinus sylvestris* L. and *P. nigra* Arn. He stated that the eggs are laid in the buds of the young apical shoots and, less frequently, in side shoots. The buds are completely destroyed by the larval feeding. The presence of the weevils in the young shoots is evidenced by yellowing of the needles. At the tips of the infested buds the larvae construct cells out of the excrement and frass that also enclose the needles. Larvae were found in these cells in May and June, and in July pupae were found there.

Distribution.— This species occurs in central, northern, eastern and southeastern Europe (Dieckmann, 1968: 479).

ANTHONOMUS SULCATUS SPECIES GROUP

Recognition.— The members of this species group are distinguished by the following characters:
1) spiculum gastrale of male genitalia with basal portion flat, not closely engaging aedeagus, without ventral keel (Fig. 70);
2) aedeagus without midventral, subbasal lobe (Figs. 55–68).

Discussion.— This group of 14 Neotropical species is probably paraphyletic. Several monophyletic subgroups of the group are evident, but relationships among these subgroups cannot be satisfactorily resolved on the basis of observed characters. Known hosts of the members of the group are species of Malpighiaceae.

Anthonomus sulcipygus Champion

Anthonomus sulcipygus Champion 1903: 177. *Lectotype* (here designated): Panamá, male [♂] [Sp. Figured.] [V. de Chiriquí/ below 4,000 ft./ Champion.] [B.C.A.Col.IV.4./ Anthonomus/ sulcipygus/ Champ.] (BMNH). *Paralectotypes*: Panamá, 2 males, 1 female [Caldera,/ 2400 ft.; Champion.] [(♂) (♂♀)] [B.C.A.Col.IV.4./ Anthonomus/ sulcipygus/ Champ.] (BMNH); 1 female [San Lorenzo,/ Panama./ Champion] [A sulcipygus/ Ch.] (BMNH). Champion 1910: 186. Champion (1903: 177) stated that *A. sulcipygus* was represented by eight specimens, all from Panamá ("Volcan de Chiriqui" and Caldera). The eight syntypes examined included specimens labelled "V de Chiriqui,""Caldera," and "San Lorenzo." The latter locality (also in the Department of Chiriquí) was not mentioned in the original description but presumably the specimen bearing that label was among the eight syntypes. Only four of the original eight syntypes represent the species described here. The other three syntypes are *A. sulcatus*.

Recognition (Figs. 13, 14).— This species is distinguished by the following combination of characters:

1) aedeagus with obliquely truncated apical projection (Fig. 55);
2) pygidial sulcus of female long, deep, well-defined (Fig. 41);
3) rostrum of female long, slender, strongly curved (Fig. 13);
4) endophallus with large proximal field of dense, minute denticles, a large tooth-like sclerite and a more distal, serrate sclerite (Fig. 55).

Characters by which *A. sulcipygus* is distinguished from the related *A. sulcatus* and *A. pimentai* are discussed under the treatment of the latter species.

Description.— Male. *Length*: 2.8–3.4 mm ($\bar{x}=3.0$, n=9). *Width*: 1.3–1.6 mm ($\bar{x}=1.4$, n=9). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: slender, length 1.6–1.8 x ($\bar{x}=1.7$, n=9) pronotal length; evenly curved; proximal portion rugose-punctate, sulci obsolete; distal portion finely, sparsely punctate, length 24–30% ($\bar{x}=27$, n=9) of total rostral length. *Thorax*: pronotum with elongate, narrow aeneous scales and middorsal vitta of broader, whitish scales. *Pygidium*: median sulcus narrow, deeper and wider apically, not reaching apex. *Legs*: profemur ca. 1.4 x stouter than metafemur; distal tooth obsolete; protibia with acute preapical tooth; metatibial uncus curved, with slight basal process.

Female. *Length*: 2.8–3.2 mm ($\bar{x}=33.0$, n=7). *Width*: 1.3–1.5 mm ($\bar{x}=1.4$, n=7). *Rostrum*: length 1.5–2.2 x ($\bar{x}=1.9$, n=7) pronotal length; strongly, evenly curved; proximal portion rugose, vestiture limited to extreme base; distal portion smooth, length 31–47% ($\bar{x}=40$, n=7) of total rostral length. *Pygidium*: with broadly rounded apicodorsal prominence; median sulcus long, deep, widened apically, with long, dense setae. *Abdomen*: sternum 5 with posterior margin nearly straight.

Plant Association.— Label data indicate that specimens of *A. sulcipygus* were collected on Malpighiaceae, *Byrsonima coccolobifolia* H.B.K. (1 specimen, reared from flower bud, Fazenda Campininha, Mun. Mogi-Guaçú, São Paulo, Brazil).

Distribution.— This species is represented by specimens from widely separated localities in México, Nicaragua, Panamá and southern Brazil. In addition to the type series from Panamá, the following specimens were examined.

BRAZIL. *Minas Gerais*: Nova Lima, *São Paulo*: Fazenda Campininha, Mun. Mogi-Guaçú (1 female, MZSP).

MEXICO. *Veracruz*: Coyame, Catemaco (2 males, TAMU). The specimens on which Champion's (1910: 186) Managua, Nicaragua, record were based have not been examined. The specimens were collected in the months of February, June and September.

Anthonomus chinculticensis, new species

Type Series.— *Holotype*: México, male [MEXICO:/ Chiapas/ Chincultic Ruins/ August 29, 1982/ Clark and Cave] (USNM).

Recognition.— This species is distinguished by the following characters:

1) aedeagus constricted subapically, rounded at narrow apex (Fig. 56);
2) endophallus with small, obtuse denticles, a large tooth, and a long serrate sclerite (Fig. 56).

It closely resembles *A. sulcipygus* but differs in characters of the male genitalia. In *A. chinculticensis* the aedeagus is narrowed distally, then slightly expanded at the extreme apex

(Fig. 56), whereas in *A. sulcipygus* the aedeagus is abruptly constricted to an obliquely truncate apical prominence (Fig. 55).

Description.— Male. *Length*: 2.7 mm (n=1). *Width*: 1.4 mm (n=1). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: length 1.5 x (n=1) pronotal length; most strongly curved over antennal insertions; proximal portion rugose-punctate, length 23% (n=1) of total rostral length. *Thorax*: pronotum with elongate, acuminate, fuscous scales, without middorsal vitta of broader, more pallid scales. *Pygidium*: median sulcus narrow, slightly wider and deeper apically; with shallow, narrow, lateral sulci. *Legs*: profemur ca. 1.4 x stouter than metafemur, with small distal tooth that shares common base with large ventral tooth; protibia with small preapical tooth; metatibial uncus large, curved, oblique, with slight prominence.

Female. Unknown.

Plant Association.— Unknown.

Distribution.— This species is known only from the type locality from southern México.

Specific Epithet.— The name of this species is derived from the name of the type locality, the site of a small Mayan pyramid.

Anthonomus vanini, new species

Type Series.— *Holotype*: Brazil, male [Rio de Janeiro/ Guanabara BRAZIL] [IX63] (MZSP). *Paratypes*: Brazil, 2 males [Rio de Janeiro/ Guanabara BRAZIL] [IX63]. Total paratypes, 2 (AUEM, TAMU).

Recognition.— This species is distinguished by the following combination of characters:

1) aedeagus slightly asymmetrical, with narrow apical projection (Fig. 57);
2) endophallus with minute denticles and two large tooth-like sclerites (Fig. 57);
3) metatibia of male without setiform scales.

It resembles *A. camoiranensis* in possession of an acute apicomedian projection on the aedeagus (Figs. 57, 58). It is distinguished from that species in lacking a dense apicoventral fringe of setiform scales on the metatibia of the male.

Description.— Male. *Length*: 2.9–3.0 mm ($\bar{x}$=3.0, n=3). *Width*: 1.2–1.5 mm ($\bar{x}$=1.4, n=3). *Head*: eyes separated by distance ca. 0.7 x width of rostrum at base. *Rostrum*: length 1.4–1.5 x ($\bar{x}$=1.4, n=3) pronotal length; most strongly curved over antennal insertions; proximal portion strongly carinate; distal portion finely, sparsely punctate, length 24–26% ($\bar{x}$=25, n=3) of total rostral length. *Thorax*: pronotum with elongate, narrow, aenescent scales and a narrow, middorsal vitta of broader, more pallid whitish scales. *Pygidium*: median sulcus narrow, wider and deeper apically. *Legs*: profemur ca. 1.3 x stouter than metafemur, with distinct distal tooth; protibia with preapical tooth; metatibial uncus minute, acute.

Female. Unknown.

Plant Associations.— Unknown.

Distribution.— This species is known only from the type series from southern Brazil.

Specific Epithet.— This species is named for Sergio A. Vanin of São Paulo, Brazil, in appreciation of his friendship and encouragement.

Anthonomus camoiranensis, new species

Type Series.— *Holotype*: Venezuela, male [VENEZUELA: Bolívar/ Gran Sabana (Camoiran)/ 19 June 1984/ W.E. Clark] [*Byrsonima/ crassifolia/* (L.) H.B.K.] (USNM).

Recognition.— This species is distinguished by the following combination of characters:

1) metatibia of male with dense apicoventral brush of long, curved, setiform scales in distal 1/2;
2) metatibia of male without apical uncus;
3) aedeagus with narrow apical projection;
4) endophallus with small distal field of moderately large denticles, one slightly larger than the other (Fig. 58).

It is distinguished from the closely related *A. vanini* by characters listed in the treatment of that species.

Description.— Male. *Length*: 2.9 mm (n=1). *Width*: 1.2 mm (n=1). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostum*: length 1.4 x (n=1) pronotal length; most strongly curved over antennal insertions; proximal portion rugose-punctate, sulci obsolete; distal portion smooth, sparsely punctate, 35% (n=1) of total rostral length. *Thorax*: pronotum with narrow, acuminate aeneous scales and middorsal vitta of broader, whitish scales. *Pygidium*: median sulcus narrow, wider and deeper apically, slightly asymmetrical. *Legs*: profemur ca. 1.2 x stouter than metafemur, with distinct distal tooth; protibia long, slender, without preapical tooth.

Female. Unknown.

Plant Association.— The holotype of *A. camoiranensis* was collected on Malpighiaceae (*Byrsonima crassifolia* (L.) H.B.K.).

Distribution.— This species is known only from the type locality in southeastern Venezuela.

Specific Epithet.— The name of this species is derived from the name of the type locality.

Anthonomus stockwelli, new species

Type Series.— *Holotype*: Panamá, male [Panamá, C.Z./ Coco solo Hosp./ 9°21′N, 79°51′W/ 20 Jan. ′72 Stockwell] (USNM). *Paratypes*: Panamá, 1 male [Panamá: Canal Zone/ Barro Colorado Is./ 9°10′N 70°50′W] [16.VII.1978/ E.M. Fisher]; 1 male [Panamá: Colon Prov./ Santa Rita Ridge/ 9°22′N, 79°44′W/ 13 June, ′76: E.G. Riley]. Total paratypes, 2 (CHAH, CWOB).

Recognition.— This species is distinguished by the following combination of characters:

1) head constricted behind large, prominent eyes (Fig. 15), transversely channelled behind frons;
2) pygidial sulcus of male narrow, not delimited apically (Fig. 34);
3) aedeagus (Fig. 59) narrowed apically to long, acuminate point;
4) endophallus unarmed (Fig. 59);
5) body form narrow (Fig. 16).

Description.— Male. *Length*: 2.2–3.0 mm (x̄=2.7, n=3). *Width*: 1.3–1.4 mm (x̄=1.4, n=3). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: length 1.1–1.4 x (x̄=1.3, n=3) pronotal length; most strongly curved over antennal insertions; proximal portion rugose-punctate, sulci obsolete; vestiture obsolete slightly proximad of antennal insertions; distal portion shallowly, finely punctate, length 17–28% (x̄=17–28% n=3) of total rostral length. *Thorax*: pronotum with elongate, acuminate, fulvous to fulvo-ferruginous scales and middorsal vitta of broader, more pallid whitish scales. *Legs*: profemur ca. 1.4 x stouter than metafemur, with distinct distal tooth; protibia without preapical tooth; metatibial uncus minute, oblique.

Female. Unknown.

Plant Association.— Unknown.

Distribution.— This species is known only from the type series from Panamá.

Specific Epithet.— The species is named for Henry P. Stockwell, collector of the holotype, in honor of his contribution to the study of the Curculionidae.

Anthonomus filicornis Hustache

Anthonomus filicornis Hustache 1929: 257. *Holotype*: Guadeloupe, female [GUADELOUPE/ Gourbeyre/ L Dufau. A. Hust.] [MUSEUM PARIS/ 1949/ Col. A. HUSTACHE] [Anth./ filicornis/ m.] (MNHP).

Recognition (Figs. 17, 18).— This species is distinguished by the following combination of characters:

1) aedeagus asymmetrical, narrowed to obtusely pointed apex (Fig. 60);
2) endophallus with minute proximal denticles, with larger denticles and a small tooth-like distal sclerite (Fig. 60);
3) pygidium of female produced and narrowed apically (Fig. 42);
4) posterior margin of female 5th abdominal sternum subtruncately produced;

5) pygidial sulcus of male with long lateral setae.

Description.— Male. *Length*: 2.4–2.9 mm ($\bar{x}$=2.7, n=12). *Width*: 1.2–1.4 mm ($\bar{x}$=1.3, n=12). *Head*: vertex minutely punctate, with whitish, setiform scales; eyes prominent in profile, round, posterior margins not elevated, separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: length 1.4–1.7 x ($\bar{x}$=1.5, n=12) pronotal length; slightly curved; proximal portion shallowly rugose, glabrous; distal portion sparsely, shallowly punctate, length 25–32% ($\bar{x}$=28, n=12) of total rostral length. *Thorax*: pronotum with narrow, acuminate to setiform, fulvous to aenescent scales and middorsal vitta of pallid, broader whitish scales. *Pygidium*: median sulcus narrow, deeper and wider apically. *Abdomen*: sternum 5 with broad, subtruncate, posterior marginal prominence. *Legs*: profemur ca. 1.3 x stouter than metafemur, distal tooth blunt; protibia with slight preapical tooth; metatibial uncus large, truncate.

Female (Figs. 17,18). *Length*: 2.8–3.0 mm ($\bar{x}$=2.7, n=15). *Width*: 1.2–1.5 mm ($\bar{x}$=1.3, n=15). *Rostrum*: length 1.5–1.8 x ($\bar{x}$=1.6, n=15) pronotal length; broadly, evenly curved; proximal portion with sulci obsolete, glabrous, except for setiform scales at extreme base; length of distal portion 30–41% ($\bar{x}$=36, n=15) of total rostral length.

Plant Associations.— Label data indicate that *A. filicornis* has been collected on the following plants:

Malpighiaceae
  Byrsonima stipulacea Adr. Juss. (5 specimens, 8 km. S Kilometro 88, Bolívar, Venezuela);
  Byrsonima spicata (Cav.) DC (2 specimens, 3 km. W La Tigrera and 5 km. N Las Trincheras, Bolívar, Venezuela).
Myricaceae
  Myrica splendens (SW) DC (1 specimen, Sainte-Rose, Piton, Guadeloupe).

It seems most likely that the *Byrsonima* are true hosts but that the *Myrica* record is an accidental association.

Distribution.— This species is represented by specimens from the Lesser Antilles, Panamá, Venezuela and Brazil. In addition to the female holotype from Guadeloupe, the following specimens were examined:

BRAZIL. *Minas Gerais*: Prata (1 female, CCBM). *Pernambuco*: Caruaru (1 male, DZUP). Goiás: Dianópolis (1 female, MZSP). *São Paulo*: Fazenda Pau d'Alho (1 male, MZSP).

GUADELOUPE. Sainte-Rose, Piton, 300 m (1 male, LFEV).

PANAMA. *Panamá*: Cerro Campana (1 male, USNM). *Cocle*: 10 mi SW. Penonome (1 male, SWOB).

VENEZUELA. *Bolívar*: 8 km. S Kilometro 88 (3 males, 2 females, AUEM); 3 km. W La Tigrera (2 females, AUEM); 5 km. N Las Trincheras (2 females, AUEM). *Delta Amacuro*: Isla C. Mánamo, 25 km. S Tacúpita (1 female, CCBM). *Guárico*: Morrocoyes (1 male, IZAV). *Lara*: Jabon (1 male, AUEM). *Portuguesa*: Mesa de Cavacas (1 male, 1 female, AUEM). *Yaracuy*: 7 km. W Nirgua (9 females, AUEM, TAMU). The specimens were collected in the months of February, April, June-August and November.

Anthonomus sulcatus Kirsch

Anthonomus sulcatus Kirsch 1874: 431. *Holotype*: Peru, female [Pozuzu/ Kirsch] [TYPUS] [Staatl. Museum für/ Tierkunde Dresden] [Anthonomus/ sulcatus Ksch.] (SMTD).

Recognition (Figs. 19, 20).— This species is distinguished by the following combination of characters:

1) aedeagus with asymmetrical apical projection (Fig. 61);
2) endophallus with sparse mesal and distal denticles and a large, proximal sclerite (Fig. 61);
3) pygidial sulcus of male narrow, shallow (Fig. 35);
4) pygidium of female with broadly rounded apical prominence, sulcus short, shallow (Fig. 44).

It is distinguished from the similar *A. filicornis* by the male genitalia (Figs. 60, 61) and the female pygidium (Figs. 42, 44). Characters by which *A. sulcatus* is distinguished from the

related *A. sulcipygus* and *A. pimentai* are listed under the treatment of the latter.

The genitalia of the males of *A. sulcatus* from México and Panamá differ from those from Brazil in having the apex somewhat constricted before the asymmetrical apical prominence.

There is uncertainty about the identity of this species because the holotype is a female and the reliability of the diagnostic characters listed cannot be ascertained while the females of related species (*A. vanini, A. camoiranensis, A. stockwelli,* and *A. chinculticensis*) remain unknown.

Description.— Male. *Length*: 2.0–2.8 mm (x̄=2.5, n=10). *Width*: 1.0–1.4 mm (x̄=1.2, n=10). *Head*: eyes prominent, separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: slender, length 1.3–1.6 x (x̄=1.5, n=10) pronotal length; broadly, evenly curved; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion finely, sparsely punctate, length 25–34% (x̄=29, n=10) of total rostral length. *Thorax*: pronotum with narrow, aeneous scales and narrow middorsal vitta of broader, more pallid scales. *Pygidium* (Fig. 35): median sulcus narrow, curved, slightly wider apically. *Legs*: profemur ca. 1.2 x stouter than metafemur; distal tooth obsolete; protibia with long, acute preapical tooth; mesotibia with ventral, subapical prominence; metatibial uncus short, truncate.

Female. *Length*: 2.3–2.8 mm (x̄=2.6, n=15). *Width*: 1.1–1.4 mm (x̄=1.2, n=15). *Rostrum*: slender, length 1.3–1.7 x (x̄=1.5, n=15) pronotal length; broadly, evenly curved; distal portion smooth, length 32–44% (x̄=37, n=15) of total rostral length. *Abdomen*: posterior margin of sternum 5 slightly produce medially.

Plant Association.— Label data indicate that the host plant of *A. sulcatus* is: Malpighiaceae, *Heteropterys xanthophylla* Adr. Juss. (3 females, reared from flower buds, Belo Horizonte, Minas Gerais, Brazil).

Distribution.— This species is known from widely separated localities in México, Panamá, Peru and Brazil. In addition to the female holotype from Peru, the following specimens were examined.

BRAZIL. *Mato Grosso*: Chapada dos Guimaraes (1 female, MPEG). *Minas Gerais*: Belo Horizonte, UFMG Campus (3 females, AUEM, MZSP); Cachoeira do Campo (3 females, AUEM, MZSP); ca 5 km. S Conceição do Mato Dentro (4 females, AUEM, MZSP); São Sebastão das Aguas Claras, Nova Lima (5 males, 20 females, AUEM, MZSP, TAMU); São Sebastão das Aguas Claras, Nova Lima (2 females, AUEM, MZSP); São Sebastão das Aguas Claras, Nova Lima (1 male, 2 females, AUEM, MZSP); Serro (4 females, AUEM, MZSP). *Rio de Janeiro*: Mt. Corcovado (1 male, 2 females, TAMU). *São Paulo*: Fazenda Pau d'Alho, Itú (1 female, MZSP); Ilha dos Buzios (1 male, MZSP). *Santa Caterina*: Nova Teutônia (1 female, ELSC).

MEXICO. *Guerrero*: 6 mi. NE Taxco (1 male, CWOB).

PANAMA. (from the type series of *A. sulcipygus*, BMNH) 1 female [(♀)] [V. de Chiriqui,/ 25–4000 ft./ Champion.] [B.C.A.Col.IV.4./ Anthonomus/ sulcipygus/ Champ.] [Type]; 1 male, 2 females [(♂♀)] [V. de Chiriqui,/ 25–4000 ft./ Champion.] [B.C.A.Col.IV.4./ Anthonomus/ sulcipygus/ Champ.]. The specimens were collected in January and September-December.

Anthonomus pimentai, new species

Type Series.— Holotype: Brazil, male [Brazil: Minas Gerais/ São Sebastão das Aguas/ Claras, Nova Lima/ 3 Sep 1984 W.E. Clark] (MZSP). *Paratypes*: Argentina, 1 male [Puerto Iguazú, m 200, MISIONES/ ARGENT. Bordón/ leg. 27 XII 1980]. Bolivia, 1 female [BOLIVIA, S.C., 10/ mi. W. Portachuelo/ March 24, 1978 at/ night CW&L O'Brien]. Brazil, 2 males, 11 females [Brazil: Minias Gerais/ São Sebastão das Aguas/ Claras, Nova Lima/ 3 Sep 1984 W.E. Clark]; 1 female [BRAZIL: M.G., São/ Sebastão das Aguas/ Claras, Nova Lima/ 16 Dec 1980 R.P. Martins] [Taken on/ Malpighiaceae/ Banisteriopsis?]; 1 female [Itapetinga/ Bahia Brazil]; 1 female [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus 4 Oct 1985/ Hélcio R. Pimenta] [reared from flower/ buds Heteropterys/ umbellata Adr. Juss. (Malpighiaceae)]; 1 female [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus 10 Oct 1985/ Hélcio R. Pimenta] [reared from flower/ buds Tetrapterys/ humilis Adr. Juss. (Malpighiaceae)]; 1 male, 8 females [Brazil: Minas Gerais/ Belo Horizonte UFMG/ campus/ N.S. Domingos] [(Stigmaphyllon/ lalandianum)/ (C15 19 Apr 82) (C13 3 Apr 81) (C13 13 Nov 81) (C4 31 Aug 81) (C15 12 Apr 82) (C13 04 Apr 82) (Banisteriopsis/ malifolia/ (15 12 Apr 82) (B17 14 Jan 82)]; 6 females [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus, Sep 1985/ Hélcio R. Pimenta] [reared from flower/ buds Heteropterys/ xanthophylla Adr. Juss. (Malpighiaceae)]; 4 females [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus, 3 Sep 1985/ Hélcio R. Pimenta] [reared from flower/ buds Tetrapterys/ humilis Adr. Juss./ (Malpighiaceae)]; 5 females [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus, 4 Oct 1985/ Hélico R. Pimenta] [reared from flower/ buds Heteropterys/ umbellata Adr. Juss./ (Malpighiaceae)]; 2 males [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus, 4 Oct 1985/ Hélcio R. Pimenta] [reared from flower/ buds Tetrapterys/ humilis Adr. Juss./ (Malpighiaceae)]; 7 females [BRAZIL: M.G., Belo/

Horizonte, UFMG/ Campus 18 May 1985/ R.P. Martins] [reared from flower/ buds Banisteriopsis/ oxyclada Adr. Juss.)./ Gates (Malpighiaceae)]; 2 males, 1 female [BRAZIL: M.G., Belo/ Horizonte, UFMG/ Campus 27 Apr 1985/ R.P. Martins] [reared from flower/ buds Banisteriopsis/ oxyclada Adr. Juss.)] / Gates (Malpighiaceae)]; 1 female [BRAZIL: M.G., Belo/ Horizonte, UFMG/ Campus 27 Apr 1985/ R.P. Martins] [reared from; Stigmaphyllon/ sp.]; 1 female [Itapetinga/ Bahia Brazil]; 2 males, 5 females [BRAZIL, Mato Grosso/ Sinop (12°31'S,/ 55°37'W) X 1974/ M. Alvarenga]; 1 male, 1 female [MACAIBA/ R.G. Norte BRASIL/ 22.VII.1951/ M. Alvarenga legit.] [Ex coleção/ M. Alvarenga]; 6 males, 9 females [Macaíba/ RN Brasil/ (1.XII.1951) (XII.1951)/ M. Alvarenga col.]; 3 males, 5 females [NATAL/ R.G. Norte Brasil/ VII 1951/ M. Alvarenga leg.] [Ex coleção/ M. Alvarenga]; 2 males, 1 female [Nova Teutônia/ SC, Brasil/ XII.1965/ F. Plaumann col.]; 8 males, 8 females [Nova Teutônia,/ Santa Catarina, Brasil (XII-15-53) (I-5-55) (I-25-55) (XII-25-55) (XII-26-56) (I-15-57) (I-25-57)] [F. Plaumann/ Collr.] [E.L. Sleeper/ Collection]; 1 male [BRASIL: S. Catarina/ Nova Teutônia/ 300-500 m/ 27°11'S 52°23'W] [-.X.1974/ F. Plaumann]; 1 male, 2 females [Dptº Zool/ UF-PARANA] [Brasilien/ Nova Teutônia/ 27°11'B. 52°23'L/ Fritz Plaumann/ 300 . 500m/ (X, 1969) (XII 1980)]; 5 males, 6 females [Brasilien/ Nova Teutônia/ 27°11'B. 52°23'L/ Fritz Plaumann/ (I 1954) (III 1954) (IV 1954) (IX 1954) (XII 1955)/ 300 . 500 m]; 1 male [Brasilien/ Nova Teutônia/ 27°11'B. 52°23'L/ Fritz Plaumann/ XI 1942/ 300 bis 500 m]; 1 male [S. Roque SP/ 25 XII.71/ F. Lane Col.]; 1 male [7.VII.1955/ Barueri/ S. Paulo/ 5465] [K. Lenko leg]; 1 female [BRAZIL: São Paulo/ Botucatu, Cerrado/ de Usina 8 Apr 1980/ P.S. Oliveira] [Taken on/ Byrsonima/ coccolobifolia]; 1 female [Barueri/ S. Paulo - Brasil/ 18.IV.1955/ K. Lenko col]. Total paratypes, 128 (AUEM, CCBM, CWOB, DZUP, ELSC, MZSP, TAMU).

Recognition (Figs. 21, 22).— This species is distinguished by the following combination of characters:

1) profemur long, stout, ventral tooth displaced distally;
2) pro- and mesocoxae and bases of profemora of male with long setiform scales;
3) aedeagus with broad, asymmetrical, emarginate, apical projection (Fig. 62);
4) rostrum of female long, slender, strongly curved;
5) pygidial sulcus of male broad, deep, carinate medially (Fig. 36);
6) endophallus with minute proximal denticles and a long, lightly sclerotized tube (Fig. 62).

The characters of the coxae and male genitalia distinguish males of *A. pimentai* from those of the related *A. sulcatus* and *A. sulcipygus*. The females of *A. pimentai* are distinguished from females of the other two species by the relatively long rostrum. Additionally, the profemur is considerably less stout in *A. sulcipygus* and also has a well-developed tooth distal to the large ventral tooth. Conversely, in *A. sulcatus*, the profemur is stout, but the stoutness is not displaced distally and there is an obsolete tooth distal to the large ventral tooth. *A. pimentai* is also distinguished from *A. sulcatus* and *A. sulcipygus* by characters of the female pygidium, but these are difficult to assess without dissection. In *A. pimentai* the impression is shallow but near the apex (Fig. 43) and visible even in specimens in which the pygidium is but narrowly exposed. In *A. sulcipygus* the pygidial channel is long, deep, and relatively well-defined (Fig. 41), whereas in *A. sulcatus* the channel is short, shallow, and displaced anteriorly so that it is visible only in specimens with the pygidium broadly exposed (Fig. 44).

The males of *A. pimentai* from Santa Catarina and from Argentina have shorter setiform scales on the pro- and mesocoxae than do those from Minas Gerais.

Description.— Male. *Length*: 2.4–3.0 mm ($\bar{x}$=2.8, n=15). *Width*: 1.1–1.4 mm ($\bar{x}$=1.3, n=15). *Head*: eyes separated by distance ca. 0.7 x width of rostrum at base. *Rostrum*: length 1.6–1.8 x ($\bar{x}$= 1.7, n=15) pronotal length; broadly, evenly curved; proximal portion sulcate, strongly carinate; distal portion finely, sparsely punctate, length 22–32% ($\bar{x}$=27, n=15) of total rostral length. *Thorax*: pronotum with elongate, narrow, aenescent scales and middorsal vitta of broader, more pallid whitish scales. *Legs*: profemur ca. 1.4 x stouter than metafemur; protibia with obsolete preapical tooth; metatibial uncus minute, acute.

Female. *Length*: 2.3–3.4 mm ($\bar{x}$=2.8, n=15). *Width*: 1.1–1.7 mm ($\bar{x}$=1.4, n=15). *Rostrum*: long, slender, length 2.0–2.3 x ($\bar{x}$=2.2, n=15) pronotal length; strongly, evenly curved; proximal portion shallowly sulcate, vestiture limited to extreme base; distal portion smooth, length 30–49% ($\bar{x}$=43, n=15) of total rostral length. *Pygidium* (Fig. 43): with broad, rounded, apicomedian prominence. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Plant Associations.— There are no published host records. Label data indicate that *A. pimentai* is associated with the following plants:

Malpighiaceae

Banisteriopsis malifolia (Nees & Mart) Gates (3 specimens, Belo Horizonte, Minas Gerais, Brazil)

Banisteriopsis oxyclada Adr. (Juss.). Gates (10 specimens, reared from flower buds, Belo Horizonte, Minas Gerais, Brazil)

Byrsonima coccolobifolia H.B.K. (1 specimen, Cerrado de Usina, Botucatu, Brazil)

Heteropterys umbellata Adr. Juss. (6 specimens, reared from flower buds, Belo Horizonte, Minas Gerais, Brazil)

Heteropterys xanthophylla Adr. Juss. (6 specimens, reared from flower buds, Belo Horizonte, Minas Gerais, Brazil)

Stigmaphyllon lalandianum (6 specimens, Belo Horizonte, Minas Gerais, Brazil)

Stigmaphyllon sp. (1 specimen, reared from flower bud, Belo Horizonte, Minas Gerais, Brazil)

Tetrapterys humilis Adr. Juss. (7 specimens, reared from flower buds, Belo Horizonte, Minas Gerais, Brazil)

Distribution.— This species is known only from the type series from southern Brazil, Bolivia and northern Argentina.

Specific Epithet.— This species is named for Hélcio R. Pimenta of Belo Horizonte, Brazil, as a token of appreciation for his help and friendship.

Anthonomus bechyneorum, new species

Type Series.— *Holotype*: Brazil, [Rio de Janeiro/ Guanabara BRAZIL] [VIII63] (MZSP). *Paratypes*: Brazil, 1 male, 3 females [Rio de Janeiro/ Guanabara BRAZIL] [VIII63]; 1 female [Guanabara, Rio/ de Janeiro Brazil]; 1 male [Corumbá de Goiás/ GO, Brasil/ 31.I.3.II.1962/ J. Bechyné col.]; 1 male, 1 female [Caraguatatuba - SP/ (Res. Flor. - 40 m)/ 2–IV–962 - Martíns/ Reichardt & Silva]; 1 male [Caraguatatuba - SP/ (Res. Flor. - 40 m.)/ 22–V. –I. VI. 1962/ Exp. Dep. Zool.]. Colombia, 1 male, 1 female (COLOMBIA) [Villavicencio/ 23–I–76/ J.A. Jimenez] [Semilla/ arbol/ maderable]. Honduras, 1 male [HONDURAS, Atl./ Liberia, 5–IX–1984/ C.W. O'Brien, rainforest]; 1 female [HONDURAS, Atl./ La Ceiba, CURLA/ 30 Aug. 1984/ C.W. O'Brien]. Trinidad, 2 males [6-1/2 mi. Post, Maracas/ Bay, Trinidad,/ W. I. Aug (8) (13), 1969/ H. & A. Howden]. Venezuela, 3 females [VENEZUELA: Tachira/ Pueblo Nuevo/ 29 June 1983; W.E. Clark and Clark]. Total paratypes, 17 (AUEM, CWOB, HAHC, MZSP, USNM).

Recognition (Fig. 23).— This species is distinguished by the following combination of characters:

1) elytra with dark middorsal macula (Fig. 24);

2) prothorax with broad scales and narrower, setiform scales;

3) scales on rostrum dense almost to antennal insertions;

4) scales on elytra not fasciculate;

5) aedeagus with asymmetrical, emarginate apical prominence (Fig. 63);

6) endophallus minutely denticulate (Fig. 63);

7) meso- and metafemora without long setiform scales;

8) pygidial sulcus of male shallow, narrow, delimited apically.

The male genitalia of *A. bechyneorum* are similar to those in *A. haliki* (Figs. 63, 64), but *A. bechyneorum* is smaller in size, has more distinct middorsal elytral macula (Figs. 24, 26), and lack long setiform scales on the male meso- and metafemora.

The males of *A. bechyneorum* from Honduras lack the apicomedian emargination of the apical prominence of the aedeagus.

Description.— Male. *Length*: 2.3–3.3 mm ($\bar{x}=3.0$, n=7). *Width*: 1.0–1.5 mm ($\bar{x}=1.4$, n=7). *Head*: eyes separated by distance ca 0.8 x width of rostrum at base. *Rostrum*: length 1.3–1.5 x ($\bar{x}=1.5$, n=7) pronotal length; most strongly curved over antennal insertions; proximal portion rugose-punctate, sulci and carinae obsolete; distal portion shallowly rugulose-punctate, length 19–33% ($\bar{x}=25$, n=7) of total rostral length. *Thorax*: pronotum with elongate, acuminate to setiform aeneous scales and with middorsal vitta of broader, more pallid fulvous scales. *Pygidium*: median sulcus narrow, wider and deeper apically. *Legs*: profemur ca. 1.4 x stouter than metafemur, with small, blunt distal tooth; protibia with short preapical tooth; metatibial uncus large, curved, with basal prominence.

Female. *Length*: 3.0–3.6 mm ($\bar{x}=3.3$, n=9). *Width*: 1.4–1.6 mm ($\bar{x}=1.5$, n=9). *Rostrum*: stout, length 1.5–1.7 x ($\bar{x}=1.6$, n=9) pronotal length; slightly, evenly curved; proximal portion rugose-punctate, vestiture extensive almost to antennal insertions; distal portion smooth, length 25–32% ($\bar{x}=30$, n=9) of total rostral length. *Pygidium*: with rounded apicodorsal prominence; median sulcus ovate, shallow, with spare, elongate scales. *Abdomen*: sternum 5 with posterior margin nearly straight.

Plant Associations.— Unknown.

Distribution.— This species is known from the type series from widely separated localities in Central and South America.

Specific Epithet.— This species is named for J. and B. Bechyné. Their efforts have resulted in great enrichment of collections of South American Curculionidae and other insects.

Anthonomus haliki, new species

Type Series.— *Holotype*: Brazil, male [Atibaia/ São Paulo./ 18.XI 1971./ F. Halik/ 11655] (MZSP). *Paratypes*: Brazil, 2 males, 5 females [Atibaia/ São Paulo./ (26.XI 1971.) (18.XI 1971) (17.XI 1971)/ F. Halik/ (11607) (11608) (11654) (11676) (11677) (11678) (11679)]. Total paratypes, 7 (AUEM, MZSP).

Recognition (Figs. 25, 26, 64).— This species is distinguished by the following combination of characters:

1) meso- and metafemora of male with long, fine, setiform scales;
2) pronotum and elytra with pallid olivaceous and slightly narrower aeneous scales;
3) elytral strial punctures oversized, giving pallid scales slightly fasciculate appearance (Fig. 26);
4) males with scales on rostrum extensive almost to antennal insertions;
5) aedeagus with asymmetrical apical prominence (Fig. 64);
6) endophallus without denticles, with a large, distal, tooth-like sclerite (Fig. 64);
7) pygidial sulcus of male narrow, delimited proximad of apex.

This relatively large *Anthomorphus* closely resembles *A. bechyneorum* in the shape of the aedeagus (Figs. 63, 64). The two species are distinguished by the larger body size, and smaller, less distinct middorsal elytral macula of *A. haliki* (Figs. 24, 26). In addition, the meso- and metafemora of the male of *A. haliki* have long setiform scales lacking in *A. bechyneorum*.

Description.— Male. *Length*: 4.0–4.1 mm ($\bar{x}=4.1$, n=3). *Width*: 2.0 mm ($\bar{x}=2.0$, n=3). *Head*: eyes separated by distance ca. 0.9 x width of rostrum at base. *Rostrum*: length 1.6–1.7 x ($\bar{x}=1.7$, n=3) pronotal length; slightly, evenly curved; proximal portion rugose-punctate, sulci obsolete; distal portion rugulose-punctate, length 18–19% ($\bar{x}=19$, n=3) of total rostral length. *Legs*: profemur ca. 1.4 x stouter than metafemur, with minute distal tooth that arises from base of large ventral tooth; protibia with short preapical tooth; metatibial uncus large, curved, with basal prominence.

Female. *Length*: 4.0–4.2 mm ($\bar{x}=4.2$, n=5). *Width*: 1.9–2.1 mm ($\bar{x}=2.0$, n=5). *Rostrum*: length 2.1–2.2 x ($\bar{x}=2.1$, n=5) pronotal length; slightly, evenly curved; proximal portion rugose-punctate, vestiture obsolete well proximad of antennal insertions; distal portion rugulose, length 36–40% ($\bar{x}=38$, n=5) of total rostral length. *Pygidium*: with rounded apicodorsal prominence; median sulcus ovate, shallow, with sparse, elongate scales. *Abdomen*: sternum 5 with posterior margin nearly straight.

Plant Associations.— Unknown.

Distribution.— This species is known only from the type series from southern Brazil.

Specific Epithet.— This species is named for its collector, F. Halik.

Anthonomus rulfoi, new species

Type Series.— *Holotype*: México, male [MEXICO: Tamaulipas/ 4 mi. W.C. Victoria/ (Cañon del Navillo)/ November 14, 1985/ P. Kovarik, R. Jones/ and K. Haack] (USNM). *Paratypes*: México, 1 male, 2 females [MEXICO: Tamaulipas/ 4 mi. W.C. Victoria/ (Cañon del Navillo)/ November 14, 1985/ P. Kovarik, R. Jones/ and K. Haack]; 1 male [Tamazunchale/ I.28.53 S(an) L(uis) Potosí)./ D.G. Kissinger]; 1 male [Jalapa, Mex./ J.T. Mason]. Total paratypes, 5 (TAMU, USNM).

Recognition (Figs. 27, 28).— This species is distinguished by the following combination of characters:

1) metasternum, abdominal sterna and meso- and metafemora with long, fine, setiform scales;
2) metatibia of male with long, straight, ventral setiform scales in distal 2/3;
3) aedeagus abruptly widened in distal 1/4 to large lateral lobes that give way distally to apical projection with apicolateral projections (Fig. 65);
4) endophallus with minute denticles and with a large tooth (Fig. 65);
5) distal profemoral tooth obsolete.

Description.— Male. *Length*: 2.5–2.6 mm ($\bar{x}=2.6$, n=3). *Width*: 1.2 mm (n=3). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: length 1.5–1.6 x ($\bar{x}=1.6$, n=3) pronotal length; most strongly curved over antennal insertions; proximal portion shallowly sulcate, feebly carinate; distal portion shallowly rugulose-punctate, length 20–21% ($\bar{x}=20$, n=3) of total rostral length. *Thorax*: pronotum with elongate, acuminate ferruginous scales and middorsal vitta of broader, white scales. *Pygidium*: median sulcus broad, slightly wider and deeper apically. *Legs*: profemur ca. 1.4 x stouter than metafemur, with minute distal tooth that shares common base with larger tooth; protibia without preapical tooth; metatibia with minute, oblique apical uncus.

Female. *Length*: 2.4–2.5 mm ($\bar{x}=2.4$, n=2). *Width*: 1.2 mm (n=2). *Rostrum*: slender, length 1.5 x ($\bar{x}=1.5$, n=2) pronotal length; slightly, evenly curved; proximal portion feebly sulcate, vestiture limited to extreme base; distal portion smooth, length 37–48% ($\bar{x}=43$, n=2) of total rostral length. *Pygidium*: subquadrate apically, broadly emarginate apicomedially; median sulcus broad, shallow. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Plant Associations.— Unknown.

Distribution.— This species is known only from the type series from northeastern México.

Specific Epithet.— This species is named for the late Mexican author Juan Rulfo.

Anthonomus abdominalis Champion

Anthonomus abdominalis Champion 1903: 178. *Holotype*: Panamá, female [San Feliz,/ Panama./ Champion] [(♀)] [B.C.A.Col.IV.4./ Anthonomus/ abdominalis,/ Champ.] [Type] (BMNH).

Recognition (Figs. 29, 30).— This species is distinguished by the following combination of characters:

1) elytra with common, middorsal fascia of dark fuscous scales (Fig. 30);
2) protibia of male with sparse fringe of long, setiform scales in distal 1/2;
3) aedeagus with asymmetrical apical prominence (Fig. 66);
4) endophallus without denticles, with a small tooth (Fig. 66);
5) pygidial sulcus of male narrow, shallow.

Description.— Male. *Length*: 2.2–2.3 mm ($\bar{x}=2.3$, n=2). *Width*: 1.0–1.1 mm ($\bar{x}=1.0$, n=2). *Head*: eyes separated by distance ca. 0.6 x width of rostrum at base. *Rostrum*: length 1.4–1.5 x ($\bar{x}=1.4$, n=2) pronotal length; broadly, evenly curved; proximal portion shallowly, irregularly sulcate, feebly carinate; distal portion finely, sparsely punctate, length 23–25% ($\bar{x}=24$, n=2) of total rostral length. *Thorax*: pronotum with elongate, acuminate, ferruginous scales and middorsal vitta of broader, whitish scales. *Pygidium*: median sulcus narrow, slightly wider and deeper apically. *Legs*: profemur ca. 1.4 x stouter than metafemur, with small distal tooth; protibia without preapical tooth; metatibial uncus large, oblique, excavated, with slight prominence.

Female. *Length*: 2.0–2.8 mm (x̄ = 2.5, n = 11). *Width*: 1.0–1.4 mm (x̄ = 1.2, n = 11). *Rostrum*: slender, length 1.4–1.6 x (x̄ = 1.5, n = 11) pronotal length; slightly, evenly curved; proximal portion feebly sulcate, vestiture limited to extreme base; distal portion smooth, length 35–41% (x̄ = 38, n = 11) of total rostral length. *Pygidium* (Fig. 45): with narrow, rounded apicodorsal prominence; median sulcus broad, deep, wider apically. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Distribution.— This species is known from Panamá, Trinidad, Venezuela and Brazil. In addition to the female holotype from Panamá, the following specimens were examined.

BRAZIL. *Rondônia*: Vilhena (1 female, MPEG). *São Paulo*: Barueri (1 female, MZSP).

PANAMA. *Canal Zone*: Barro Colorado Island (4 females, CWOB); Barro Colorado Island (2 females, CWOB); Albrook Forest Site, Fort Clayton (1 male, CWOB); 5 mi. NW Gamboa (1 male, 2 females, USNM). *Panamá*: Pacora (1 female, USNM); Panamá (1 female, USNM). TRINIDAD. Morne Bleu (1 female, HAHC). VENEZUELA. *Aragua*: 4.5 km. SE Villa de Cura (1 female, AUEM). The specimens were collected in February, April, May, July, August, and October-December.

Anthonomus diamantinaensis, new species

Type Series.— *Holotype*: Brazil, male [Brazil: Minas Gerais/ Diamantina/ 5 September 1984/ W.E. Clark] (MZSP). *Paratypes*: Brazil, 3 males, 10 females [Brazil: Minas Gerais/ Diamantina/ 5 September 1984/ W.E. Clark]; 1 male [Brazil: Minas Gerais/ São Sebastão das Aguas/ Claras, Nova Lima/ 3 Sep 1984, W.E. Clark]; 1 male, 1 female [BRAZIL: M.G. São/ Sebastão das Aguas/ Claras, Nova Lima/ 16 Dec 80 R.P. Martins] [Taken/ on/ Malpighiaceae/ Banisteriopsis?]; 1 male, 1 female [BRAZIL: M.G., São/ Sebastão das Aguas/ Claras, Nova Lima/ 27 Feb 81 R.P. Martins] [Taken/ on/ Malpighiaceae]; 1 male, 3 females [BRAZIL: Minas Gerais/ Belo Horizonte UFMG/ Campus, 4 Oct 1985/ Hélcio R. Pimenta] [reared from flower/ buds Heteropterys/ umbellata Adr. Juss./ (Malpighiaceae)]; 2 males, 1 female [BRAZIL: M.G./ Cardeal Mota/ 17 Sept. 1985/ Clark & Martins]; 2 males [BRAZIL: M.G./ Diamantina/ 13 Sept. 1985/ Clark & Martins]; 1 male [BRAZIL: M.G./ Lagoa Santa/ 12 Sep 80, b.f.111/ R.P. Martins] [?Taken/ on/ Banisteria/ maritiana]; 3 females [BRAZIL: Minas Gerais/ MG040 Lagoa Santa/ 18 Oct 1985 R.P. Martins/ Hélcio R. Pimenta] [reared from flower/ buds Heteropterys/ umbellata Adr. Juss./ (Malpighiaceae)]; 1 male [BRAZIL: M.G./ Mendanha/ 13 Sept. 1985/ Clark & Martins]; 3 males, 2 females [BRAZIL: M.G./ Serro/ 12 Sept. 1985/ Clark & Martins]; 1 female [Pirineus/ GO, Brasil/ 2.II.1962/ J. Bechyné col.]; 2 females [Cristalina, 1200m/ GOIAS, Brasil/ Bordón 16 XI 83]; 1 female [BRASIL: Est. São Paulo, São Paulo/ 9.XII.1965/ V.N. Alin]; 1 female [BRASIL: Est. São/ Paulo, São Paulo/ 2. 1968/ V.N. Alin]; 1 male, 2 females [Brazil: São Paulo/ Faz. Campininha/ Mun. Mogi-Guaçú/ 15 November 1979] [R.P. Martins/ *Byrsonima/ intermedia/* Cerrado]; 1 female [BRAZIL: São Paulo/ Botucatu, Cerrado/ de Usina 8 Apr 1980/ P.S. Oliveira] [Taken on/ Byrsonima/ coccolobifolia]; 3 males, 1 female [BRAZIL: São Paulo/ Fazenda Campininha/ Mun. Mogi-Guaçú/ 15 Feb 1979 R.P. Martins] [Taken on/ B./ intermedia]; 1 male [DPTº ZOOL/ UF-PARANA] [BATATAIS - SP./ BRASIL 4/I/67/ Pe. J. Moure leg]; 1 female [DPTº ZOOL/ UF-PARANA] [BATATAIS - S P/ BRASIL - 6-II-1966]; 1 female [Faz. Pau d'Alho/ Itu, SP, Brasil, XI.1960/ U R. Martins col.]. Total paratypes, 52 (AUEM, CCBM, CHAH, CWOB, DZUP, MZSP, TAMU).

Recognition (Figs. 31, 32).— This species is distinguished by the following combination of characters:

1) pygidium without median sulcus (Fig. 46);
2) aedeagus abruptly constricted subapically, with slight apical projection (Fig. 67);
3) endophallus with long, thin-walled tubular sclerites (Fig. 67);
4) elytral interspace 3 prominent at extreme base.

The male genitalia of *A. diamantinaensis* are very similar to those of *A. rosadonetoi* (Figs. 67, 68), the male of which has a well-developed pygidial sulcus. No characters were found that distinguish the females of the two species.

Description.— Male. *Length*: 1.9–2.4 mm (x̄ = 2.2, n = 15). *Width*: 1.0–1.2 mm (x̄ = 1.1, n = 15). *Head*: eyes separated by distance ca. 0.8 x width of rostrum at base. *Rostrum*: length 1.3–1.8 x (x̄ = 1.4, n = 15) pronotal length; most strongly curved over antennal insertions; proximal portion deeply sulcate, strongly carinate; distal portion finely, sparsely punctate, length 24–36% (x̄ = 30, n = 15) of total rostral length. *Thorax*: pronotum with elongate, narrow, aenescent scales and middorsal vitta of broader, whitish scales. *Pygidium*: subtruncate apically. *Legs*: profemur ca. 1.3 x stouter than metafemur, without distal tooth; protibia with large, acute preapical tooth; metatibial uncus minute, acute.

Female. *Length*: 2.0–2.5 mm (x̄ = 2.3, n = 15). *Width*: 1.0–1.3 mm (x̄ = 1.1, n = 15). *Rostrum*: short, stout, length 1.3–1.7 x (x̄ = 1.5, n = 15) pronotal length; broadly, evenly curved; proximal portion deeply rugose, vestiture limited to extreme base; distal portion smooth, length 25–42% (x̄ = 32, n = 15) of total rostral length. *Pygidium* (Fig. 46): with broad, subquadrate, apicodorsal prominence. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Plant Associations.— Label data indicate that *A. diamantinaensis* has the following host plants of the family Malpighiaceae:

> *Banisteriopsis maritiana* (Adr. Juss.) Cuatr. (1 specimen, Lagoa Santa, Minas Gerais, Brazil).
>
> *Byrsonima coccolobifolia* H.B.K. (1 specimen, Cerrado de Usina, Botucatu, São Paulo, Brazil)
>
> *Byrsonima intermedia* (7 specimens, Fazenda Campininha, Mun. Mogi-Guaçú, São Paulo, Brazil)
>
> *Heteropterys umbellata* Adr. Juss. (7 specimens, reared from flower buds, Belo Horizonte and Lagoa Santa, Minas Gerais, Brazil).

Distribution.— This species is known only from the type series from southern Brazil.

Specific Epithet.— The name of this species is based on the name of its type locality.

Anthonomus rosadonetoi, new species

Type Series.— Holotype: Brazil, male [Rio de Janeiro/ Guanabara BRAZIL] [X-63] (MZSP). Paratype: Brazil, 1 female [Rio de Janeiro/ Guanabara BRAZIL] [X-63] (MZSP).

Recognition.— This species is distinguished by the following combination of characters:

1) male with broad, deep, setose pygidial sulcus;

2) female pygidium not sulcate;

3) aedeagus abruptly constricted subapically, with slight apical projection (Fig. 68);

4) endophallus with long, thin-walled tubular sclerites (Fig. 68);

5) elytral interspace 3 prominent at extreme base.

The only character distinguishing this species from *A. diamantinaensis*, aside from slight differences in the aedeagus (Figs. 67, 68), is the sulcate male pygidium. The female of *A. rosadonetoi* is indistinguishable from that of *A. diamantinaensis*.

Description.— Male. *Length*: 2.2 mm (n=1). *Width*: 1.1 mm (n=1). *Head*: eyes separated by distance ca. 0.7 x width of rostrum at base. *Rostrum*: length 1.4 x (n=1) pronotal length; most strongly curved over antennal insertions; proximal portion strongly carinate, with broad, densely punctulate, shallow sulci; distal portion rugulose, length 26% (n=1) of total rostral length. *Thorax*: pronotum with elongate, narrow, aenescent scales and middorsal vitta of slightly broader whitish scales. *Pygidium*: median sulcus narrow, wider and deeper apically. *Legs*: profemur ca. 1.3 x stouter than metafemur, with obsolescent distal tooth; protibia with short, blunt preapical tooth; metatibial uncus minute, acute.

Female. *Length*: 2.4 mm (n=1). *Width*: 1.1 mm (n=1). *Rostrum*: short, stout, length 1.6 x (n=1) pronotal length; broadly, evenly curved; proximal portion deeply rugose, vestiture limited to extreme base; distal portion smooth, length 33% (n=1) of total rostral length. *Pygidium*: with broad, subquadrate, apicodorsal prominence. *Abdomen*: sternum 5 with posterior margin slightly produced medially.

Plant Association.— Unknown.

Distribution.— This species is known only from the type series from southern Brazil.

Specific Epithet.— This species is named for Germano H. Rosado-Neto of Curitiba, Brazil, in appreciation of his help and friendship.
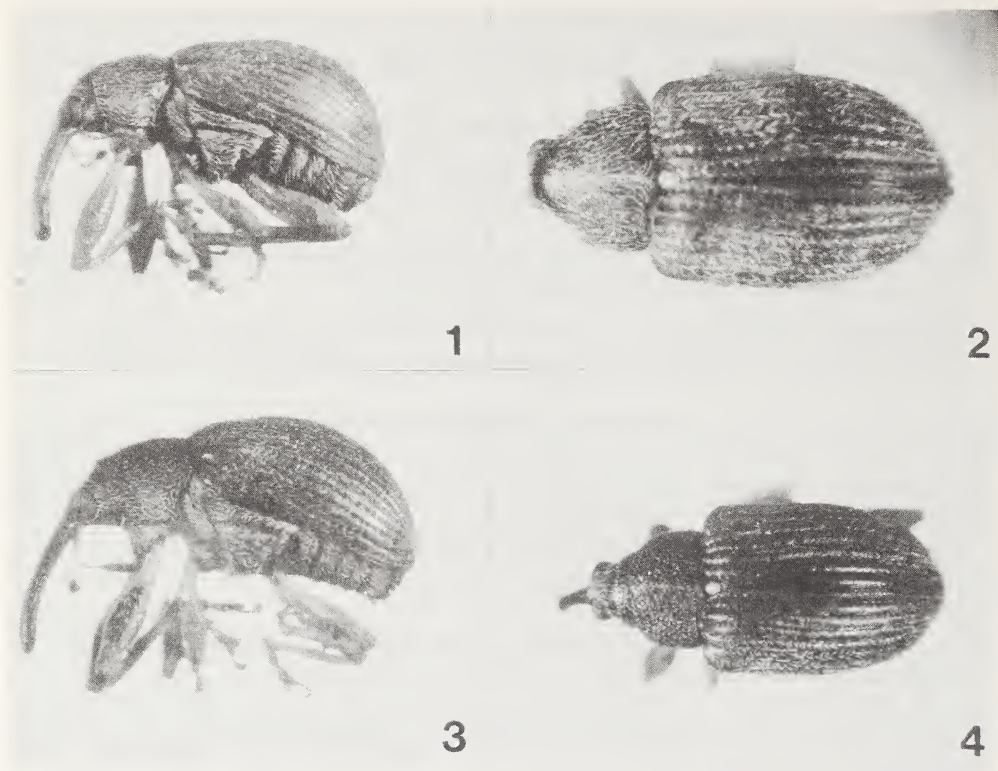
Figures 1–4. Habitus, dorsal and lateral views: 1, *A. rubidus*, male, Haddon Heights, New Jersey; 2, *A. rubidus*, male, Kappa, Illinois; 3 and 4, *A. bordoni*, male, Jaji, Venezuela.
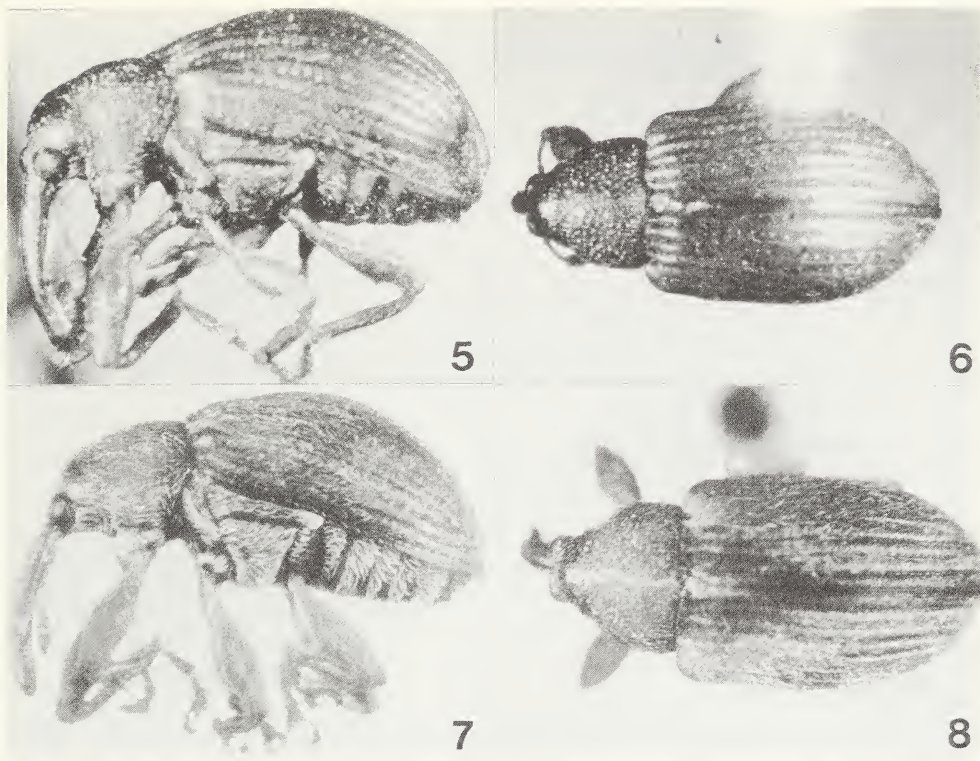
Figures 5–8. Habitus, dorsal and lateral views: 5, *A. profundus*, female, Trinity Co., California; 6, *A. profundus*, male, Ontario, Canada; 7 and 8, *A. galphimiae*, male, holotype.
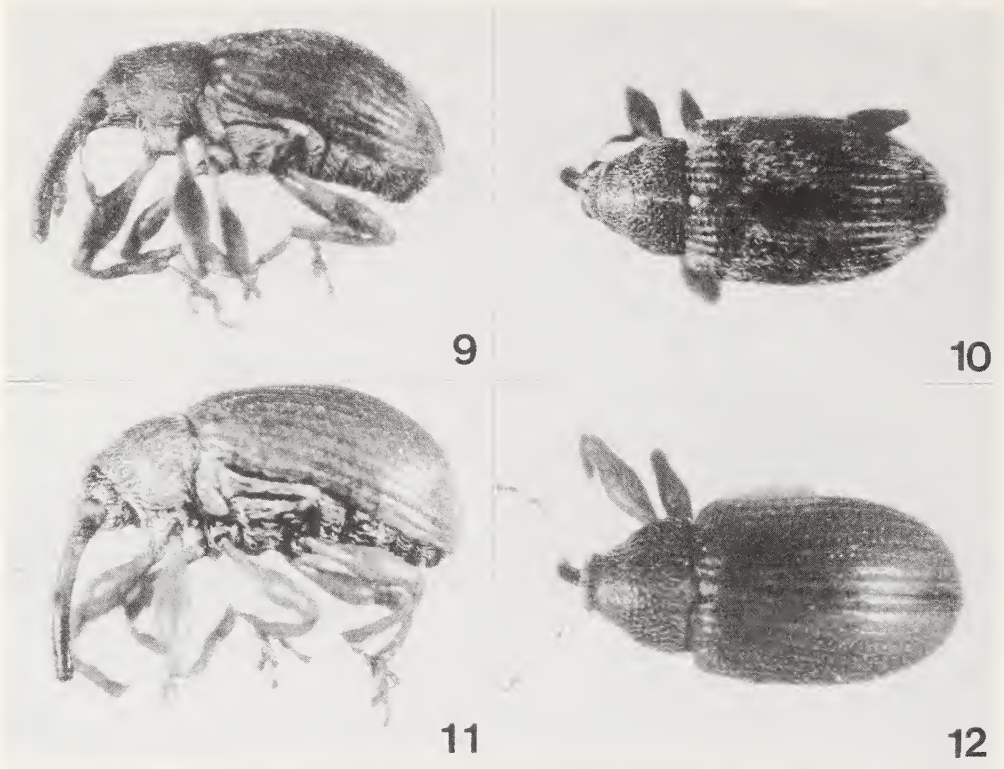
Figures 9–12. Habitus, dorsal and lateral views: 9 and 10, *A. howdenorum*, male, holotype; 11 and 12, *A. varians*, female, Ermenonv.
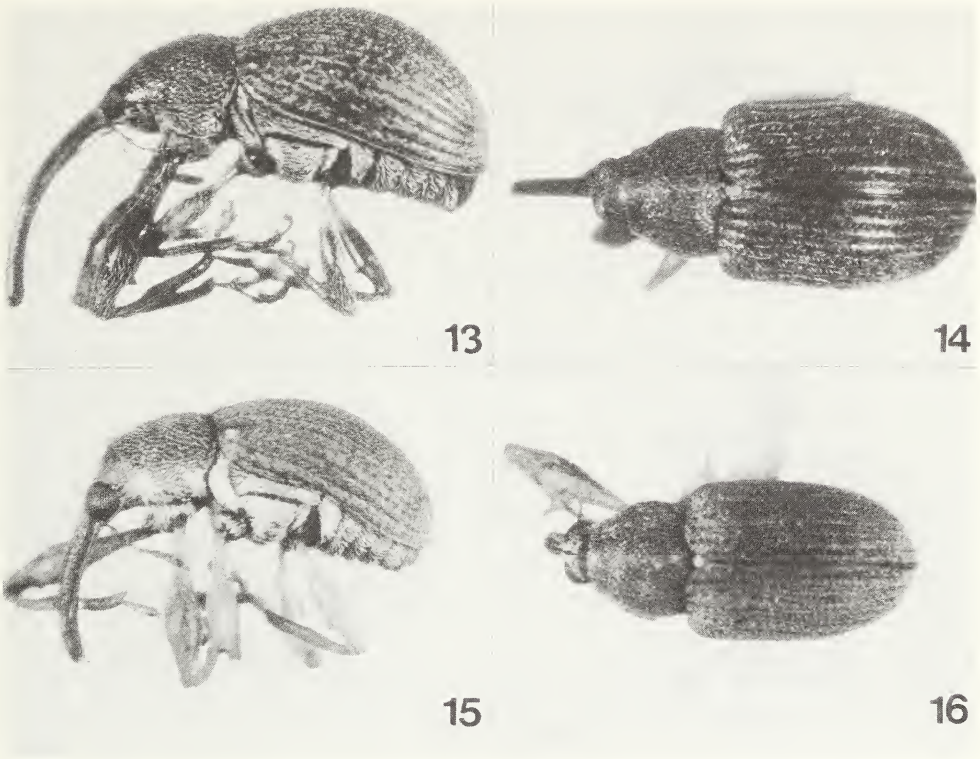
Figures 13–16. Habitus, dorsal and lateral views: 13 and 14, *A. sulcipygus*, female, São Sebastão das Aguas Claras, Nova Lima, Minas Gerais, Brazil; 15 and 16, *A. stockwelli*, male, holotype.
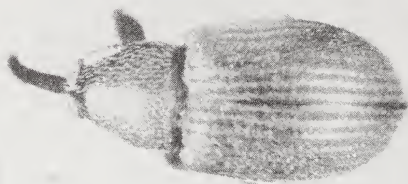
Figures 17–20. Habitus, dorsal and lateral views: 17 and 18, *A. filicornis*, female, holotype; 19 and 20, *A. sulcatus*, female, holotype.
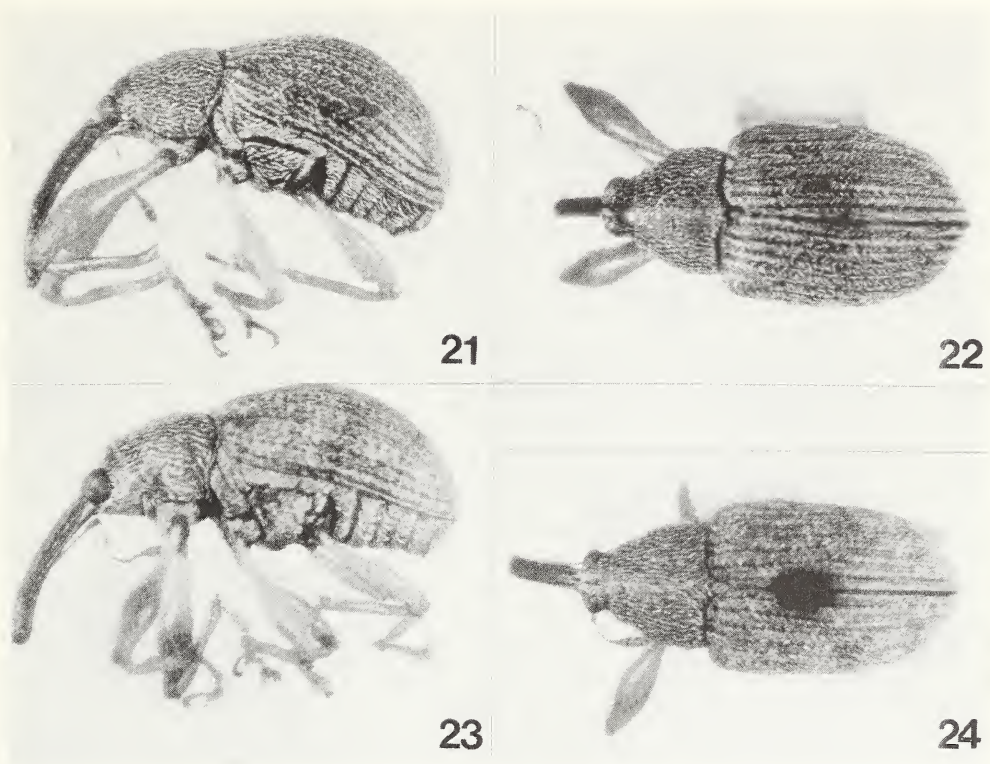
Figures 21–24. Habitus, dorsal and lateral views: 21 and 22, *A. pimentai*, male, holotype; 23 and 24, *A. bechyneorum*, male, holotype.
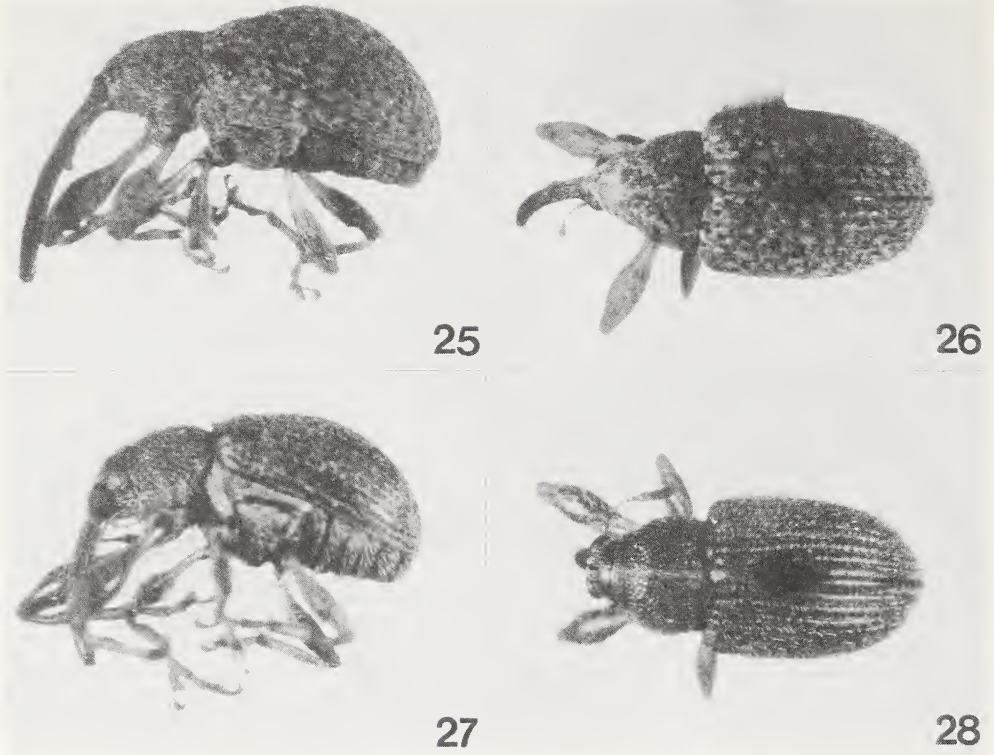
Figures 25–28. Habitus, dorsal and lateral views: 25 and 26, *A. haliki*, female, paratype; 27 and 28, *A. rulfoi*, male, holotype.
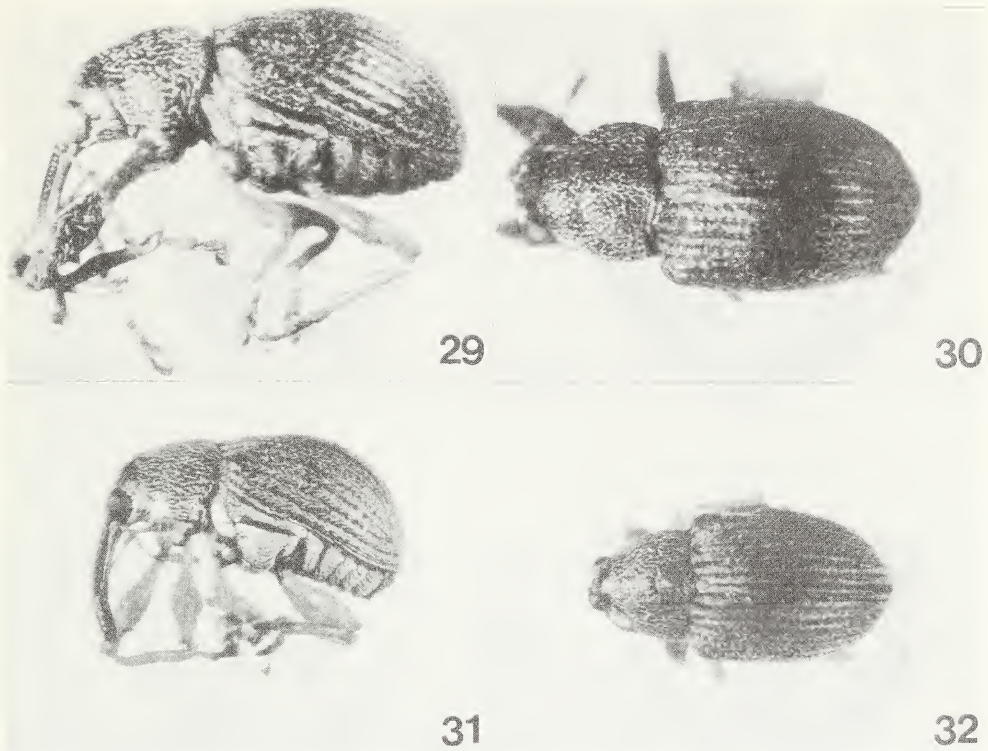
Figures 29–32. Habitus, dorsal and lateral views: 29 and 30, *A. abdominalis*, female, holotype; 31 and 32, *A diamantinaensis*, male, holotype.
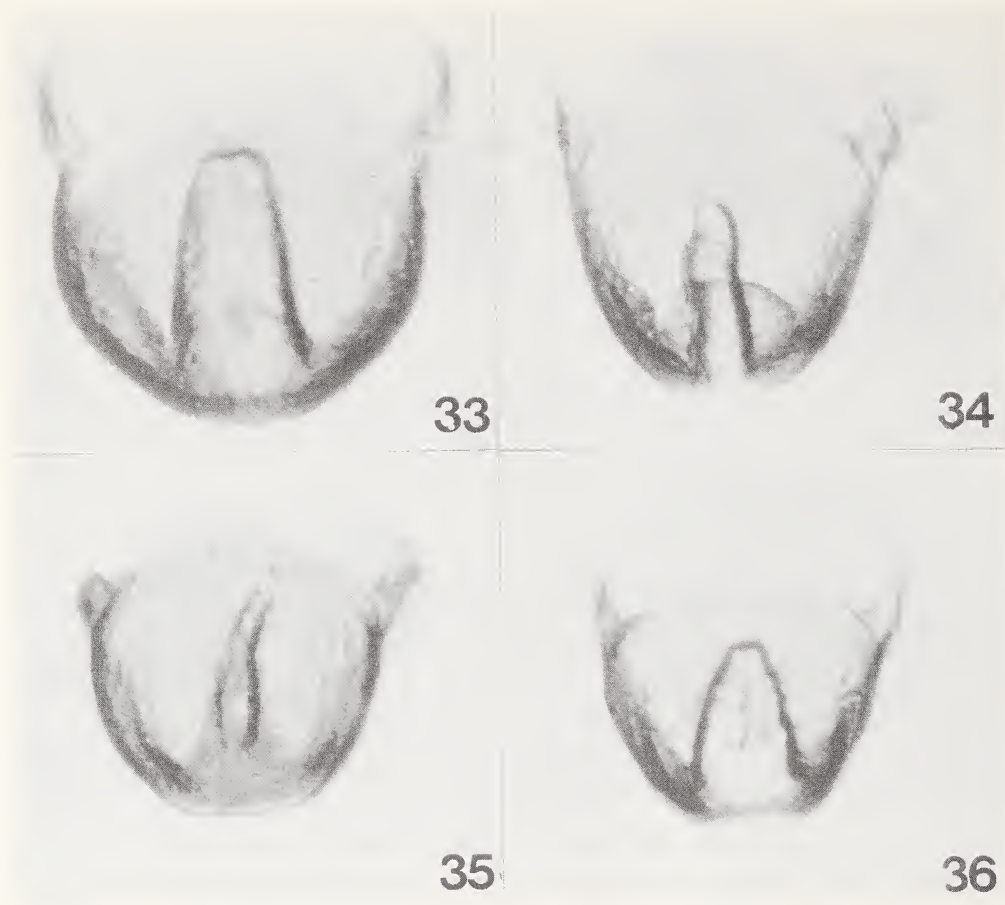
Figures 33–36. Pygidium of male, dorsal view: 33, *A. profundus*, Pocohantas Co., West Virginia; 34, *A. stockwelli*, holotype; 35, *A. sulcatus*, São Sebastão das Aguas Claras, Nova Lima, Minas Gerais, Brazil; 36, *A. pimentai*, holotype.
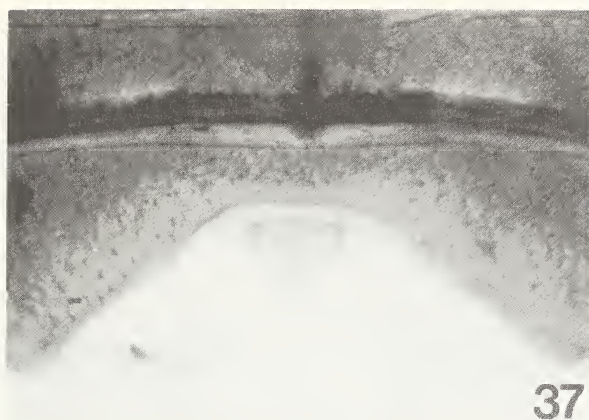
Figure 37. Fifth abdominal sternum of male, ventral view: 37, *A. filicornis*, 8 km. S Kilómetro 88, Bolívar, Venezuela.
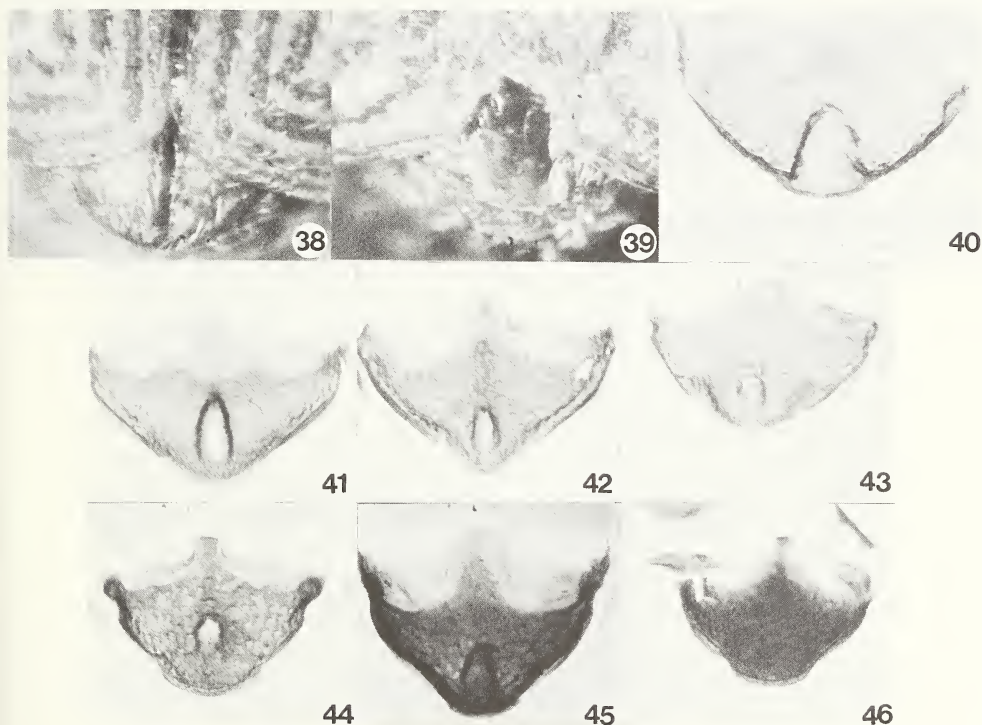
Figures 38–46. Pygidium of female, dorsal view: 38, *A. rubidus*, Tippecanoe Co., Indiana; 39, *A. profundus*, Trinity Co., California; 40, *A. galphimiae*, paratype; 41, *A. sulcipygus*, São Sebastão das Aguas Claras, Nova Lima, Minas Gerais, Brazil; 42, *A. filicornis*, 8 km. S Kilómetro 88, Bolívar, Venezuela; 43, *A. pimentai*, São Sebastão das Aguas Claras, Nova Lima, Minas Gerais, Brazil; 44, *A. sulcatus*, holotype; 45, *A. abdominalis*, holotype; 46, *A. diamantinaensis*, Diamanthina, Minas Gerais, Brazil.
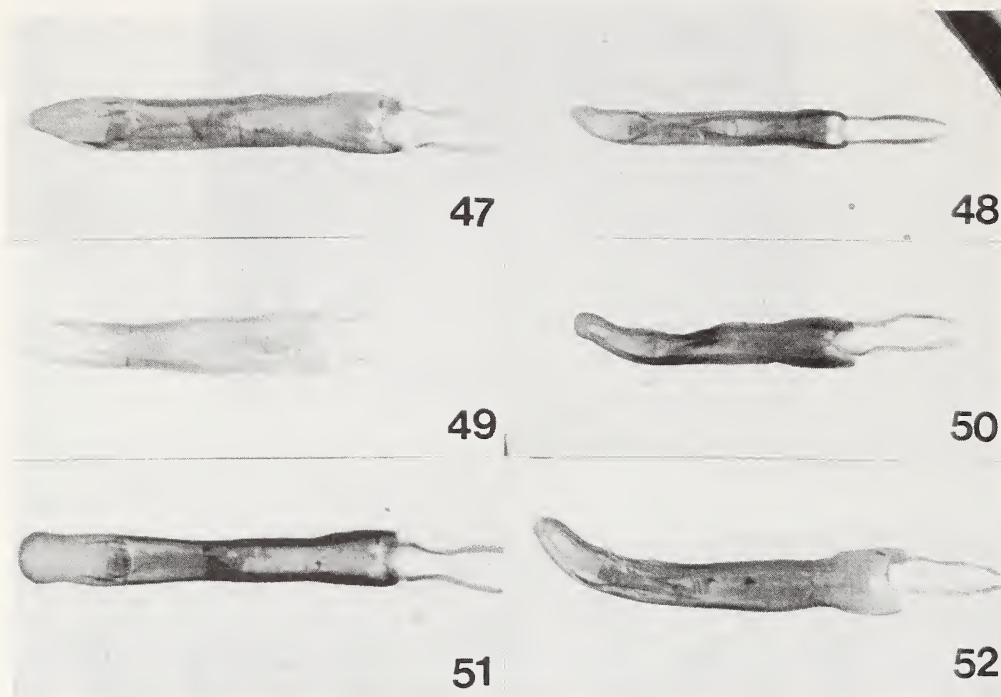
Figures 47–52. Aedeagus, dorsal view: 47, *A. rubidus*, Kappa, Illinois; 48, *A. bordoni*, holotype; 49, *A. paraguayanus*, Nova Teutônia, Santa Catarina, Brazil; 50, *A. profundus*, Pocohantas Co., West Virginia; 51, *A. galphimiae*, holotype; 52, *A. howdenorum*, holotype.
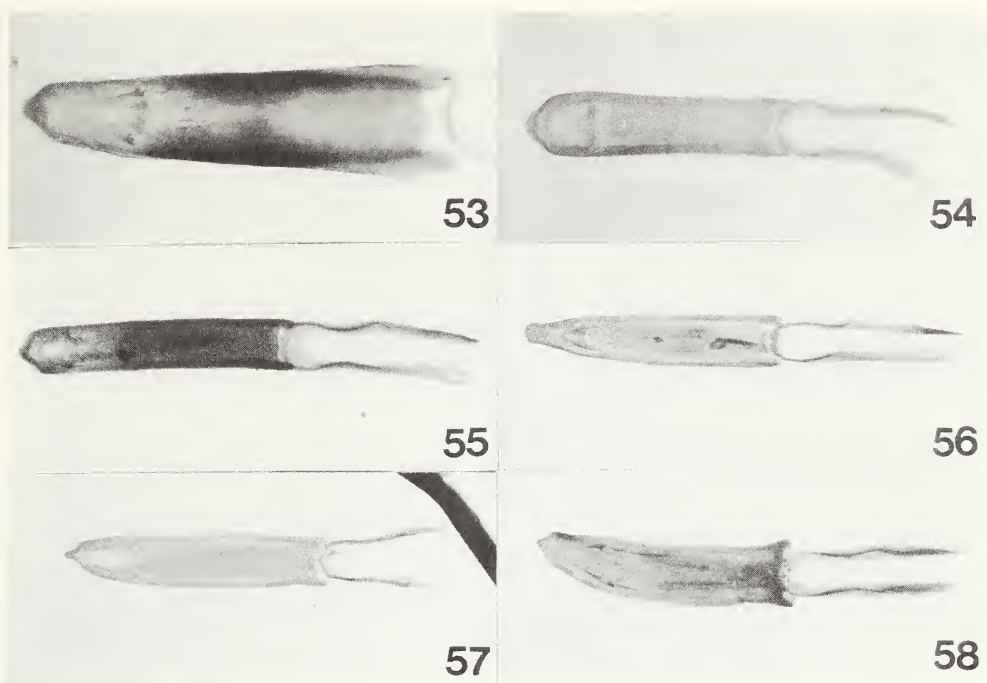
Figures 53–58. Aedeagus, dorsal view: 53, *A. varians* Ermenonv; 54, *A. pinivorax*, Europe; 55, *A. sulcipygus*, São Sebastão das Aguas Claras, Nova Lima, Minas Gerais, Brazil; 56, *A. chinculticensis*, holotype; 57, *A. vanini*, holotype; 58, *A. camoiranensis*, holotype.
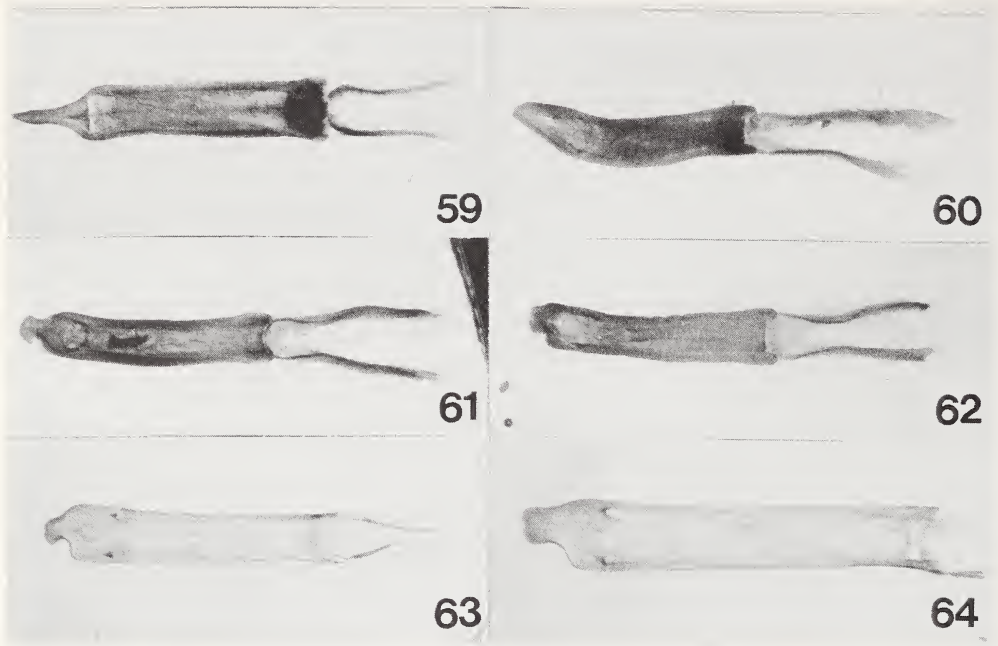
Figures 59–64. Aedeagus, dorsal view: 59, *A. stockwelli* holotype; 60, *A. filicornis*, 8 km. S Kilometro 88, Bolívar, Venezuela; 61, *A. sulcatus*, São Sebastão das Aguas Claras, Nova Lima, Minas Gerais, Brazil; 62, *A. pimentai*, holotype; 63, *A. bechyneorum*, holotype; 64, *A. haliki*, holotype.
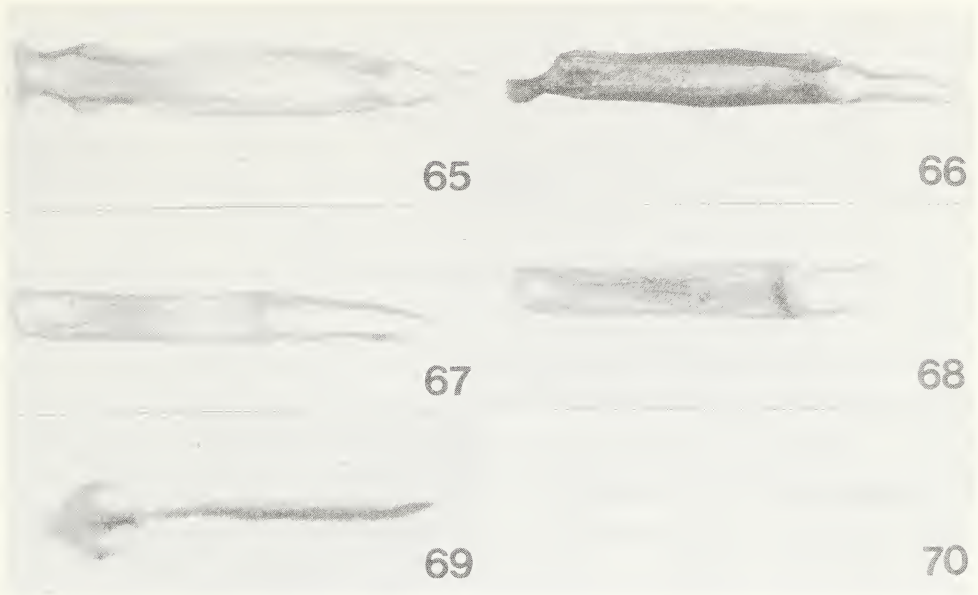
Figures 65–68. Aedeagus, dorsal view: 65, *A. rulfoi*, holotype; 66, *A. abdominalis*, 5 mi. NW Gamboa, Canal Zone, Panamá; 67, *A. diamantinaensis*, holotype; 68, *A. rosadonetoi*, holotype.

Figures 69–70. Spiculum gastrale of male genitalia, ventral view: 69, *A. bordoni*, holotype; 70, *A. vanini*, holotype.

PHYLOGENETIC RELATIONSHIPS

General Considerations

Phylogenetic relationships of the species of *Anthomorphus* were determined by comparing the distribution of morphological characters of the adult stage of each of the species. Twenty-seven of these characters (listed in Table 1) were determined to be apomorphic by comparison of the species of *Anthomorphus* with a hypothetical ancestral taxon. This taxon, or outgroup, was conceptualized after examination of numerous anthonomines, including members of the *grandis, gularis, unipustulatus* and *venustus* groups of the genus *Anthonomus* and the *Anthonomus* subgenus *Anthonomorphus* (see Clark, 1987 and Clark and Burke, 1985; 1986a, b.). The distribution of apomorphic characters (presence indicated by a score of "1," absence by a score of "0") among the 22 species of *Anthomorphus* is depicted in Table 2.

The characters were analyzed using the PAUP computer programs for the species consistent with the distribution of characters determined to be apomorphic, thus minimizing the number of required hypotheses of homoplasy. The result, compromised by weighting some characters to give a pattern only partly consistent with that produced by PAUP, is the phylogenetic tree depicted in Fig. 71.

The analyses are in three separate sets: 1) analyses of all species of *Anthomorphus* together; 2) separate analyses of the species assigned to the *rubidus* group; and 3) separate analyses of the species assigned to the *sulcatus* group. The same outgroup (lacking apomorphic characters, Table 2) was specified in each analysis. The three sets of analyses are discussed separately in the following paragraphs.

Analyses, set 1. These analyses provided the rationale for recognizing two species groups, a monophyletic *rubidus* group and a paraphyletic *sulcatus* group. An initial PAUP analysis considered all of the species of *Anthomorphus* with a unique set of apomorphic characters (*i.e.,* one each of each of pairs of taxa 6 and 15, 9 and 11, 10 and 19, and 13 and 18 in Table 2 was deleted from the analysis), using the MULPARS option. This analysis produced more than 100 equally parsimonious trees. A strict consensus tree derived from these trees indicated that the species assigned to the *rubidus* group, except for *A. varians* and *A. pinivorax*, belong to a single monophyletic group. A subsequent PAUP analysis (also using the MULPARS option) treated the same species as did the first, except that *A. pinivorax* (taxon 14) was excluded. The consensus tree derived from the trees produced by this analysis placed *A. varians* in the *rubidus* group at the position indicated in Fig. 71. The problematical *A. pinivorax* is depicted in Fig. 71 as the sister group of *A. varians* on the basis of synapomorphy in characters 1, 2, 7, 24, 26, even though subsequent PAUP analyses weighting these characters failed to move that species to the *rubidus* group.

Set 2, the *rubidus* group. As constructed by the analyses described as set 1, this group is justified on the basis of synapomorphous characters 12 and 13 (see Table 1). The species in this group (taxa 4, 12–14, 16, 18, 21 and 23) were subjected to a PAUP analysis using the ALLTREES option without weighting. This analysis produced a single tree with the topology depicted in the upper portion of Fig. 71.

The problems encountered in formulation of this group stem from the fact that *A. varians* and *A. pinivorax* seem to have diverged considerably from the New World stock from which they must have been derived. The greatest problem is that *A. pinivorax* does not exhibit the apomorphic characters (12 and 13) indicating monophyly of the group to which it is assigned. The problem is compounded by the absence in *A. pinivorax* of the emargination of sternum 5 of

```
                                              27 ┌───── rubidus
                                           14 ┌───┤
                                        ┌──────┤   └───── bordoni
                                        │      └─────(10) paraguayanus
                       3 10 20          │        9 ┌──(10) profundus
                    ┌──────────┬────────┤     ┌────┤
                    │          │        │  4 15│    └──(15) galphimiae
          12 13     │          │        └──────┤
        ┌───────────┤          │               └──────── howdenorum
        │           │       1 2 7 24 26 ┌────────────── varians
        │           │      ┌────────────┤
        │           └──────┤            └───(11 12 13) pinivorax
        │                  │  21 ┌──────────────────── sulcipygus
        │                  └─────┤
        │                        └──────────────────── chinculticensis
        │              17 ┌────────────────────── vanini
        │           16 ┌──┤
        │         ┌─────┤  └────────────────────── camoiranensis
        │      22 │     └────────────────────(22) stockwelli
        │     ┌───┤
        │     │   ├────────────────────────────── filicornis
        │     │   └────────────────────────────── sulcatus
   8 11 │     │        19 ┌──────────────────── pimentai
  ──────┤     │      ┌────┤     6 ┌──────────── bechyneorum
        │     │      │    └───────┤
        └─────┤      │            └──────────── haliki
              │  18 23│   ────────────────(10) rulfoi
              └───────┤
                      │   ──────────────────── abdominalis
                 5 25 │   ──────────────────(8) diamantinaensis
                      └───┤
                          ─────────────────── rosadonetoi
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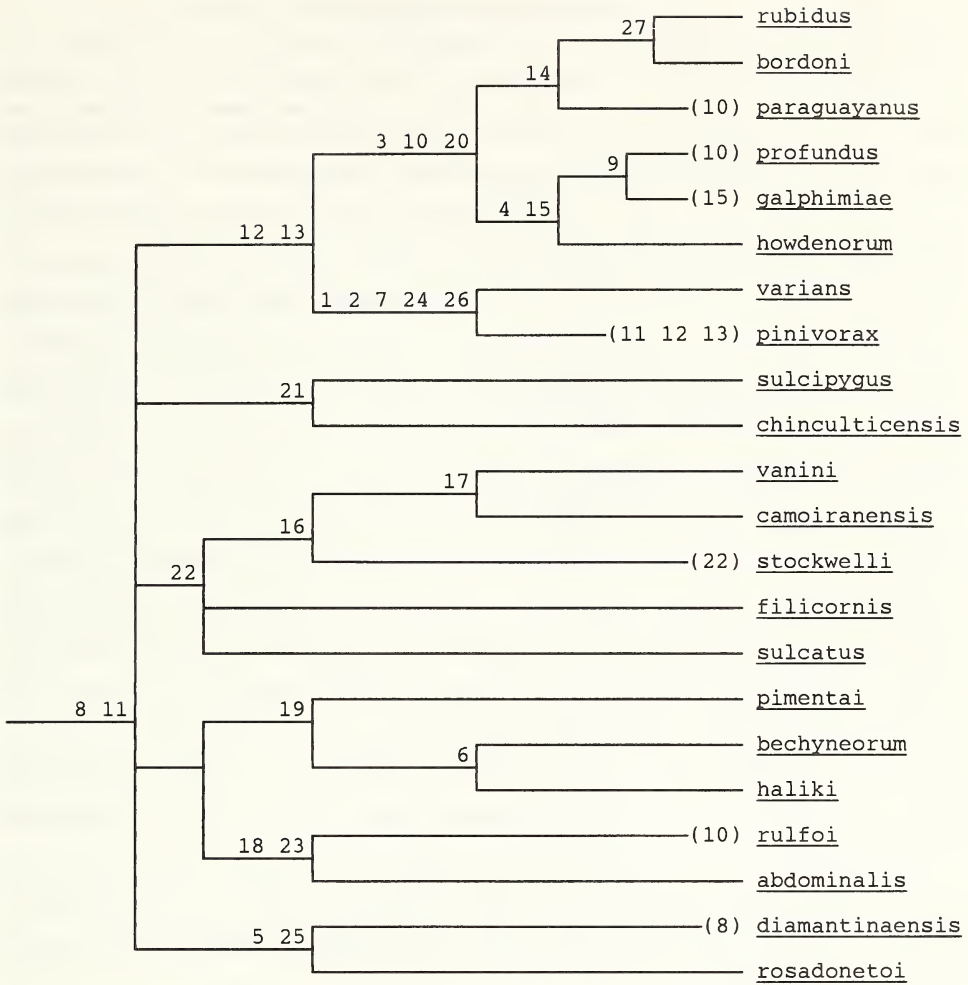
XX characters
(XX) homoplasious characters

71

Figure 71. Phylogenetic tree depicting hypothesized relationships of the species of *Anthomorphus*.

the male abdomen with the associated isolated triangular sclerite (apomorphic character 11), one of the characters considered to be synapomorphic in *Anthomorphus*. Furthermore, *A. varians* is autapomorphic for *Anthomorphus* in possession of simple tarsal claws. It is possible that *A. varians* and *A. pinivorax* are not sister species and that the apomorphic characters they share (1, 2, 7, 24 and 26) are due to convergence incidental to adaptation to similar host plants (both species are unusual among known anthonomines in having hosts in the family Pinaceae). It seems unlikely, however, that two independent host shifts involving relatively distantly related species would result in this unusual host association.

Set 3, the *sulcatus* group. A PAUP analysis was performed on the species assigned to the *sulcatus* group (taxa 2, 3, 5–10, 11, 15, 17, 19, 20, deleting one each of each of the redundant pairs of taxa 6 and 15, 9 and 11 and 10 and 19). This analysis also produced more than 100 equally parsimonious trees. The strict consensus tree derived from these trees was accepted in part. This tree indicated that *A. abdominalis*, *A. rulfoi*, *A. bechyneorum*, *A. haliki* and *A. pimentai* form a monophyletic group. This grouping was accepted even though there is no synapomorphy to support it. An analysis of these taxa to the exclusion of all of the others except the outgroup, using the ALLTREES option, produced three trees, the topology of one of which is produced as part of Fig. 71. The consensus tree also depicted *A. diamantinaensis* on a branch of its own as the sister group of all of the remainder of the *sulcatus* group. That species, however, is depicted in Fig. 71 as forming a monophyletic group with *A. rosadonetoi* on the strength of shared possession of characters 5 and 25, of which the latter is considered the strongest evidence of the suggested relationship. This arrangement requires the assumption of the loss of character 8 in *A. diamantinaensis*. The consensus tree based on the trees produced in the initial analysis of all of the species of *Anthomorphus*, described above as "Set 1," placed two of the species assigned to the *sulcatus* group, *A. sulcipygus* and *A. chinculticensis*, in the position of sister group to the *rubidus* group. There is no character evidence to support this and it is not incorporated into Fig. 71. Thus, the *sulcatus* group stands as an incompletely resolved paraphyletic group.

Further resolution of the phylogenetic relationships of the species in the *sulcatus* group cannot be made without additional characters. At this point it does not seem advisable to extend the character matrix to include additional adult morphological characters that probably would only add homoplasies.

ACKNOWLEDGMENTS

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Table 1. Apomorphic characters analyzed to produce phylogenetic tree in Fig. 71 (see Table 2)

1   Eyes small, round, prominent
2   Rostrum slender, smooth, glabrous from base to tip
3   Elytra with triangular basal macula
4   Sutural elytral interspaces expanded subapically
5   Elytral interspace 3 prominent at extreme base
6   Elytral striae large, deep
7   Scales on elytra sparse, setiform, whitish
8   Pygidium of male sulcate
9   Pygidium of female with sulcus broad, apical, posteriorly undelimited
10   Metasternum and abdominal sterna of male with long setiform scales
11   Sternum 5 of male abdomen emarginate, leaving setose, triangular sclerite
     isolated from posterior margin
12   Basal portion of spiculum gastrale embracing median lobe, keeled ventrally
13   Aedeagus with midventral, subbasal lobe
14   Aedeagus with apical portion asymmetrical
15   Aedeagus strongly asymmetrical
16   Aedeagus expanded at extreme base
17   Aedeagus with acute apicomedian projection
18   Aedeagus narrowed to base, lateral plates thick
19   Aedeagus with asymmetrical, medially emarginate, apical projection
20   Endophallus with spinose proximal plate with s-shaped component, and
     with a more distal spine
21   Endophallus with large distal spine and large serrate proximal spine
22   Endophallus with small distal spines, a larger distal spine, and a ribbed
     plate
23   Endophallus without denticles, with one small spine
24   Endophallus unarmed
25   Endophallus with long, thin-walled tubular sclerites
26   Femora inflated
27   Meso- and metafemora of male with long, ventral, setiform scales

Table 2. Data matrix for the phylogenetic tree in Fig. 71

		Characters
		0000000001111111111122222222
		1234567890123456789012345 67
01	outgroup	0000000000000000000000000000
02	*abdominalis*	0000000100100000001000010000
03	*rosadonetoi*	0000100100100000000000000100
04	*howdenorum*	0011000101111010000100000000
05	*rulfoi*	0000000101100000001000010000
06	*bechyneorum*	0000010100100000000100000000
07	*stockwelli*	0000000100100001000000000000
08	*diamantinaensis*	0000100000100000000000000100
09	*camoiranensis*	0000000100100001100000100000
10	*filicornis*	0000000100100000000000100000
11	*vanini*	0000000100100001100000100000
12	*paraguayanus*	0010000100111100000010000000
13	*bordoni*	0010000101111100000010000001
14	*pinivorax*	1100001100000000000000001010
15	*haliki*	0000010100100000000100000000
16	*profundus*	0011000110111010000100000000
17	*chinculticensis*	0000000100100000000001000000
18	*rubidus*	0010000101111100000010000001
19	*sulcatus*	0000000100100000000000100000
20	*sulcipygus*	0000000100100000000001000000
21	*varians*	1100001100111000000000001010
22	*pimentai*	0000000100100000000100000000
23	*galphimiae*	0011000111111000000010000000

INDEX TO NAMES OF TAXA
(Synonyms in italics)

BOOK REVIEW

Mitchell, Andrew W. with forward by Gerald Durrell, 1986. The Enchanted Canopy: A Journey of Discovery to the Last Unexplored Frontier, the Roofs of the World's Rainforests. Macmillan Publishing Company. New York. 225 pages, 99 colour photographs, one black and white photograph, one text figure, subject index. Price $29.95. U.S.A.

A few months before my first trip to the tropical rainforests, I accepted with great pleasure a chance to review a book on the subject of rainforest canopies, the inside front cover of which began: "you are about to enter the earth's last uncharted frontier", hopefully referring to rainforests and not the book itself. Opening the cover, I found an incredible collection of superb colour photographs, many of them entomological, but portraying among them all conceivable facets of the rainforest environment. I flipped through the pictures numerous times (and wondered if the picture at the top of page 99 was in sideways) before settling down to the text, prefaced by a brief, if uninspired, forward by Gerald Durrell.

Andrew Mitchell is an adventurer, naturalist, and television and film producer, and his book is a semi-popular treatment of life, both human and otherwise, in the world's rainforests. It is not scientific, but it does claim to represent the cutting edge of rainforest knowledge, and is therefore worthy of close scrutiny. The preface includes a vivid description of daybreak in the Bornean forest canopy, and the first chapter then presents a summary of the location and status of the world's rainforests. The tone is set, with emphasis on conservation, primates, and caving ropes. Apparently, the best way to reach the canopy is *via* ropes of the same sort used by spelunkers when lowering themselves into caves. In a harness which can be moved up and down on a main rope, biologists can suspend themselves at any level of the canopy, dangling with both arms free to take pictures, notes, or specimens. This is indeed interesting, but by the end of the book the wonders of caving ropes have been repeated *ad nauseam*, along with accounts of construction of walkways in the canopy. The second chapter is concerned with animal locomotion in the canopy. It begins with an odd argument that nightmares involving a fall from a great height, a common theme for most of us, might represent a sort of racial memory from our arboreal ancestry: one of Mitchell's erroneous views of human nature and evolution, which in my opinion form the intellectual core of this book. A discussion follows of the use of regular routes through the canopy by branch-running mammals, which reminded me of the routes taken in aspen forests around Edmonton by red squirrels. Throughout the text, naturalist readers will be reminded of temperate examples of many of the supposedly unique features of the rainforest canopy. A few inaccuracies also surface in this chapter, notably near the middle of page 44 where one gets the impression that lorises are not primates.

The third chapter, entitled "The Hanging Gardens", deals with epiphytic plants and their associated fauna, and is highlighted by a fascinating discussion of arboreal roots. It is more interesting than the preceding two chapters, perhaps on account of its dramatic, law-of-the jungle theme. The next chapter, "A Place to Live", continues the theme of dramatic competition among the forest creatures. The most entomologically interesting part of this chapter is a discussion of passion flower vines and their defences against egg-laying by heliconiid butterflies. Chapter five, "Tree-top Voices", points out the difficulty of communicating in the dense growth of the canopy, and surveys the diversity of animal calls which have evolved to use the "sound window" between 125-600 Hz, in which calls can penetrate the forest to maximum advantage. A lengthy discussion of primate calls leads to a brief discussion of orangutan sexuality, in which Mitchell uncritically cites reports of male

orangutans raping human women, and being brought to "tribal long-house parties to indulge in some bizarre activities, so much so that there was for a time a fear that venereal disease might enter the wild population." Primatologists I questioned on this topic found it as difficult to believe as I did, although orangutans are apparently the only non-human primates which engage in forced copulation. Similar sexual prowess was once mistakenly attributed to male gorillas (for an historical summary, see "Man and Apes" by Ramona and Desmond Morris, 1966, Hutchinson and Co., Ltd., London, pp. 54-83) and this belief may tell us more about our perceptions of apes than it does about great ape behaviour. This point aside, the fifth chapter is well-focussed and interesting, a welcome change for the better. "The Flowering of the Forest", the sixth chapter, begins by outlining some of the puzzles surrounding the study of canopy flowers. How do conspecifics achieve cross-pollination, and some, synchronized blooming, when they are spread few and far between among other trees? Just as this story is picking up Mitchell launches into another advertisement for caving ropes, followed by scattered natural history notes having something or other to do with pollination. The next chapter, "Feasting in the Tree Crowns", emphasizes plant dispersal and seed success, not feeding by animals as the title suggests, and includes numerous fascinating accounts of adaptations of canopy plants and animals. It wanders a bit (for example into a discussion of nesting in hornbills), misidentifies the beetle figured on page 171 as a scarab (it is a chrysomelid), and anthropomorphically refers to "terrified" ants having their brains eaten away by parasites, "sending them mad".

By the time I reached Chapter Eight ("Killers in the Canopy") it was clear that Mitchell views nature as a dramatic stage upon which violent battles are fought; a typical approach for television nature programmes, and programmers. Nonetheless, I enjoyed the interesting survey of research on carrion feeding vultures and their keen sense of smell, allowing them to find carrion hidden beneath the canopy. The last two chapters deal with people and their relationship with the rainforest. The "Tree People" presents a survey of people who "have not altogether lost the art of climbing", and thus begins with an anthropological fallacy, bordering on racism. Uncritical references to the Tasaday tribe, which is now widely considered an anthropological hoax, further tarnish Mitchell's credibility. The entire chapter seems to reflect his perception of native people as noble savages, in harmony with their surroundings and in sharp contrast with the ignorance of Western culture. Anthropologists now recognize this belief as a prime example of Western ignorance. The book ends with a plea for conservation, in a chapter with two titles; one in the table of contents ("A Future Above the Tree Tops") and one in the text ("Above the Future Forest"), both of which sound a bit religious to me. Mitchell makes a provocative point when he suggests that promotion of nature reserves in third world countries is simply "a new form of colonialism", which is true in a strictly political and sociological sense, notwithstanding good biological reasons for such endeavours. The text then produces the only two typographic errors I could find ("scaffoldng" on p. 236, and "Mavins" on p. 247), and a string of endorsements for "The Living Planet", David Attenborough ("the world's most famous naturalist"), Operation Raleigh, and a few other adventurous canopy projects, all of which involve "arboreal naturalists", fulfilling their "deeper felt mission". A complex metaphor summarizes our plight. Man is cutting off the branch he is sitting on in the great clock of the rainforest which tells us that time is up, and that we must fix the clock without knowing how it works.

Reading this book is like taking a guided hike through the rainforest canopy with a good naturalist. Along the way he points out curious plants and animals, and tells fascinating stories about them, making the hike much more informative than it would have been without him.

When we return to the starting point, we have picked up his contagious enthusiasm for the plight of this environment, and feel a strong need to do something about it. As a former interpretive naturalist myself, I admire his technique, but I also know how tempting it is to present an embellished, oversimplified version of biology in order to motivate the people on your hike. Popularization is not inherently bad, but it carries an intellectual responsibility, which Mitchell has not entirely heeded.

Why review such a book in the first place, you might ask? Certainly it is unfair for a practising biologist to pounce on a popular account as if it were a scientific treatise. On the contrary, I argue that popular science is more important than that. Those of us interested in evolutionary theory, and in the study of ecology know all too well that many of our colleagues have received most if not all of their training in these fields from their television sets, and the magazine rack. Well-educated, intelligent people will read this book, and will find little wrong with its outlook. It is extremely rare to see evolutionary theory portrayed accurately in science, let alone in the popular press. By understanding popular conceptions of ecology and evolution, we can identify sources of some of the misconceptions which arise in classrooms, biological journals, and politics.

Competition plays a strong role in Mitchell's book. Survival of the fittest, and the struggle for existence both imply the overriding importance of competition, and so evolution is seen by many people as nothing but competition. This makes for good stories. It also reinforces the idea that all life is struggling, presumably to become more advanced, which means more mammalian, or more human. In Chapter 4 we find that "amphibians suffer from the fact that their skins are permeable to water." Should we feel sorry for them, happily wrapped in our own water-tight epidermis? In the next chapter, we see that gibbons are on the right track, since they "have now chosen a family way of life." The Great Chain of Being still figures prominently in popular ideas.

Then, there is natural selection, which apparently requires sex and rainforests. One poor plant, mentioned on page 87, "is denied the genetic diversity that sex would bring, and seems to be locked into an evolutionary dead end." On page 218, we find the incredible statement that "without freedom of choice, natural selection is made sterile and evolution is brought to an end." By freedom of choice he means genetic diversity, but these concepts are not identical. Freedom of choice implies free will, or self determination. Natural selection is never prevented from choosing, it can only be restricted in the number of choices available at a given time. But "the heartland of natural selection", the rainforest, is being destroyed. What is natural selection, in Mitchell's view? On page 232, Mitchell reflects: "it is hard to believe that mere accident, moulded by a length of time beyond the imagination of our short-lived human minds, could realize such diversity." A creationist could have written that sentence, and creationists could quote it in support of their cause, if Mitchell were a more prominent evolutionist. Mis-quoting might not be necessary. Indeed, "it is hard to believe ..."

Evolutionary theory is not based on accident, it is based on selection and heritable variation. It is not based on sex, or there would be no parthenogenetic or asexual organisms. It is not based on rainforests, or there would be a wasteland outside my window in Edmonton right now. But how are non-biologists to know this, if it is the privileged knowledge of a scientific elite? The political battle between creationism and evolutionary thought no longer needs biology, since it is a popular concept of evolution which is under attack, and a lay public which defends it. I have criticised Mitchell's presentation of biology, but why should I assume that he is accountable to biologists? Perhaps this is no longer our concern, and perhaps we cannot change

either side of public opinion.

I will not end on a critical note. We cannot change the popular view of evolution, and we cannot save the rainforests from today's population pressures. Mitchell's book reflects our grief, and our collective confusion about the processes which operate in our world. On page 187, Mitchell states; "entomologists, I find, appear uninterested in most things unless insects are involved." Appearances, I hope, have proven themselves deceiving.

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BOOK NOTICE

BELLÉS, X. 1985. Sistematica, filogenia y biogeografia de la subfamilia Gibbiinae (Coleoptera: Ptinidae). Treballs del Museu de Zoologia, Núm. 3, 94 pp. Ajuntament de Barcelona. (Parc de la Ciutadella Apt. de Correus 593, 08003– Barcelona, Spain).

This number, the third to be published in a series that began in 1979, is an excellent example of modern systematic entomology, treating a taxon that is of interest to applied entomologists as well as to taxonomists and evolutionary biologists, generally. The taxonomic section contains excellent line drawings of male genitalia and habitus illustrations of many species. Dot maps complement statements in the text about geographical range of each species. The treatments of phylogenetic and biogeographic aspects of the gibbiine ptinids seem to be very well done. A valuable feature of this publication for anglophones is an English two-page summary of the Spanish text.

Treballs del Museu de Zoologia is a new series continuing the "Trabajos del Museo de Zoologia de Barcelona". An English translation of an editorial preceding the text of Bellés explains that the series is intended for publication of extensive monographic research works on any zoological group. Authors are invited to write in such a way that the text will be "easily understood by specialists of any branch of Biology". Because the editorial was translated into English, I assume that the journal is likely to accept manuscripts in languages other than Spanish. The potential importance of this series is thus apparent to authors seeking a place of publication for first class manuscripts in systematic biology.

G. E. Ball

BOOK REVIEW

D'Abrera, B., 1987. Sphingidae Mundi. E.W. Classey Ltd., Faringdon, Oxon., U.K. ix + 226
   pages, incl. Appendix, generic index, species index. 97.50 pounds sterling (inclusive)
   (approximately CAN $220.00).

This latest contribution from Mr. D'Abrera is a significant piece of work for those of us with
a love of the Sphingidae. This is not a revision of the family; it is designed to enable the reader
to identify hawk moths by comparison with the figures. There are no keys or illustrations of
genitalia.

The family is covered very well in this book. The author estimates the family contains 1050
species in approximately 200 genera; of these, only three genera and 124 species are not
illustrated here (diagnoses are provided for six of these species). From this standpoint, this is
the most complete work available on the Sphingidae.

The quality of the figures for which the author is responsible is excellent; leafing through the
plates is a delight in itself! Species are illustrated life size, the figures are clear, and colours are
accurately represented. Described subspecies are listed in the text, and although most are not
illustrated, a brief diagnosis is usually provided. An attempt has been made to show the known
variation of some species, and the dorsal and ventral surfaces of many species are illustrated. A
general distribution and some biological notes are provided. The author has included figures of
some species he has not seen in an Appendix; the quality of these figures varies, but most are
adequate.

Several taxonomic changes have been proposed: four names are proposed as new synonyms;
four names are resurrected from synonymy; one new subspecies is described; one new name is
proposed; and one lectotype is designated.

My only major complaint with this book is that, for the price, it is not particularly well
organized. The arrangement of figures on the plates may look nice in a collection, but doing this
in a book leaves a great deal of unused space. Considering the bulk of the cost of production
must be from producing the plates, leaving unused space only increases the number of plates,
and thus increases the cost of the book. The quality of the figures and the ability of the reader
to identify the species is not affected by the number or arrangement of specimens on the plate.
Since the author bore the entire cost of production himself, I am surprised a more economical
format was not adopted. Also, for several reasons, I can not see that anything has been gained
by including some figures in an Appendix; the author has not consistently placed all figures for
which he is not responsible into the Appendix (see photographs of *Philodia astyanor* Boisduval,
page 128, and *Temnora kala* Darge, page 148, and the painting of *Barbourion lemaii* (Le
Moult), page 89); the author appears to have forgotten which species are in the Appendix (see
below); and the species illustrated in the Appendix are well separated from section of text
relevant to them. With better organization of the plates, the species figured in the Appendix
could easily have been incorporated into the existing plates, thus reducing the number of plates
required (and the cost of the book).

In addition to the organization of the plates, I found it difficult to cross reference the plates
with the text. Finding the section of text relevant to a given species required scanning for a
specific name on one to three pages. Numbering the plates and adding a number to the species
name of each plate (with a corresponding number in the text) would make it much easier to
associate text and plates.

Finally, I noted that the format used for presenting data about the distribution and number of species in each genus was changed on page 86 for no apparent reason. This is a minor point, but I prefer the text to be consistent throughout.

The book has several other small defects. First, the checklist of genera has not been consistently followed in the text. *Neococytius* Hodges, *Ampeloeca* R. & J. and *Sphingidites* Kernbach are listed in the checklist, but do not appear in the text. (*Ampeloeca* is treated as a synonym of *Darapsa* Walker; *Sphingidites* is a fossil.) *Chlaenogramma* Smith and *Isogramma* R. & J. (= *Autogramma* Jordan) from the checklist are listed in the text as synonyms of *Manduca* Hübner and *Ceratomia* Harris respectively. *Cressonia* Grote & Robinson is used in the checklist and on the plate, but *Amorpha* Hübner (the correct name) is used in the text. *Compsogene* R. & J. from the checklist is equivalent to *Amblypterus* Hübner in the text; the latter does not appear in the checklist and should be spelled *Amplypterus* (it is the correct name for this genus). On other matters in the checklist, *Neoclanis* Carcasson is listed twice, and the author of *Adhemarius* is cited as "Hübner" in the checklist and "Oiticica" in the text.

Second, there are many typographical errors in the text, and although most are minor, few pages of text have no such errors. The plates are much better in this regard, but several spelling errors were noted.

Third, several oversights were noted. The text indicates the following species are illustrated in the Appendix, but figures were not found in the copy before me: *Protaleuron rhodogaster* R. & J., *Cephonodes banksi* Clark, *Cephonodes novebudensis* Clark, *Macroglossum buruensus* Holland, *Macroglossum albolineata* Clark, *Macroglossum bruini* Clark, *Macroglossum haslami* Clark, *Macroglossum moecki* Rütimeyer, and *Macroglossum stevensi* Clark. The following species are figured in the Appendix, but this is not mentioned in the text: *Oxyambulyx immaculata* Clark, *Platysphinx bituberculatus* Darge, *Polyptychus ferroseus* Gehlen, *Baniwa yavitensis* Lichy, *Xylophanes haxairei* Cadiou and *Theretra tessmanni* Gehlen. Three species are figured on the plates which are not mentioned in the text: "*P. boisduvali*" (p. 67), "*H. saundersi*" (p. 115) and "*Platysphinx dorsti*" (Appendix). *Polyptychoides grayi assimilis* R. & J. is figured on page 69; this is not mentioned in the text (p. 74), and the character in the wing maculation cited as diagnostic for this subspecies does not agree with the figure. *Leucostrophus hirundo* (Gerstaecker) is renamed *L. alterhirundo* by the author (p. 168), but *L. hirundo* is used on the plate. *Panacra cingulata* Clark from the text (p. 136) has apparently been called *P. angulata* on the plate. The figure captions for *Daphnis dohertyi* Rothschild (p. 127) and *Maasenia heydeni* (Saalmüller) (p. 139) indicate that more than one subspecies has been described for these species, but none are listed in the text. *Adhemarius gannascus dentoni* Clark from the text (p. 49) is treated as a full species on the plate (the author believes this subspecies is a separate species). In the text, *Hemeroplanes gracilis* Jordan (p. 100) also appears in the combination *Callionima gracilis* Jordan (p. 102). Finally, "Butler, 1877" is cited as the author of *Sphinx perelegans* Hy. Edwards (p. 40).

I also object very strenuously to the author's treatment of "*Cocytius cluentius* Cramer, 1775 stat. rev." (p. 22). Since this is the type species of *Neococytius* Hodges, what the author has done, in effect, is synonymize *Neococytius* and *Cocytius*. However, he has done this without even citing the name *Neococytius* in the text, and the discussion of *characters* upon which this decision was based is entirely inadequate to allow the reader to make an informed decision about the validity of *Neococytius*. His arbitrary action is scientifically unacceptable and is likely to cause confusion in the mind of the average reader. Personally, I do not think this synonymy should be accepted until D'Abrera has provided a much more detailed explanation

for this proposed change.

In spite of these criticisms, this book is an important synopsis of the Sphingidae of the world, and will be indispensible to those of us who collect hawk moths. Unfortunately, the hefty price tag may discourage many people from buying this book.

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BOOK NOTICE

COX, J. M. 1987. Pseudococcidae (Insecta: Hemiptera). Fauna of New Zealand [number] 11, 230 pages. Science Information Publishing Centre, DSIR, P. O. Box 9741, Wellington, New Zealand (US$ 29.82).

The 116 species of Pseudococcidae (67 newly recorded and 61 new to science) known to occur in New Zealand are treated in about 100 pages of text, complemented with 119 pages of excellent illustrations, showing both habitus and detailed structural features of many species. Only females are keyed and described, since males are known for very few species. Known host plant records are listed for each mealy bug species in the text, and the mealy bugs recorded for each known host plant are listed in an appendix.

This volume is another excellent contribution to the entomological literature, meeting in all respects the high standards required by the Editorial Advisory Group and the Series Editor of the "Fauna of New Zealand".

G. E. Ball
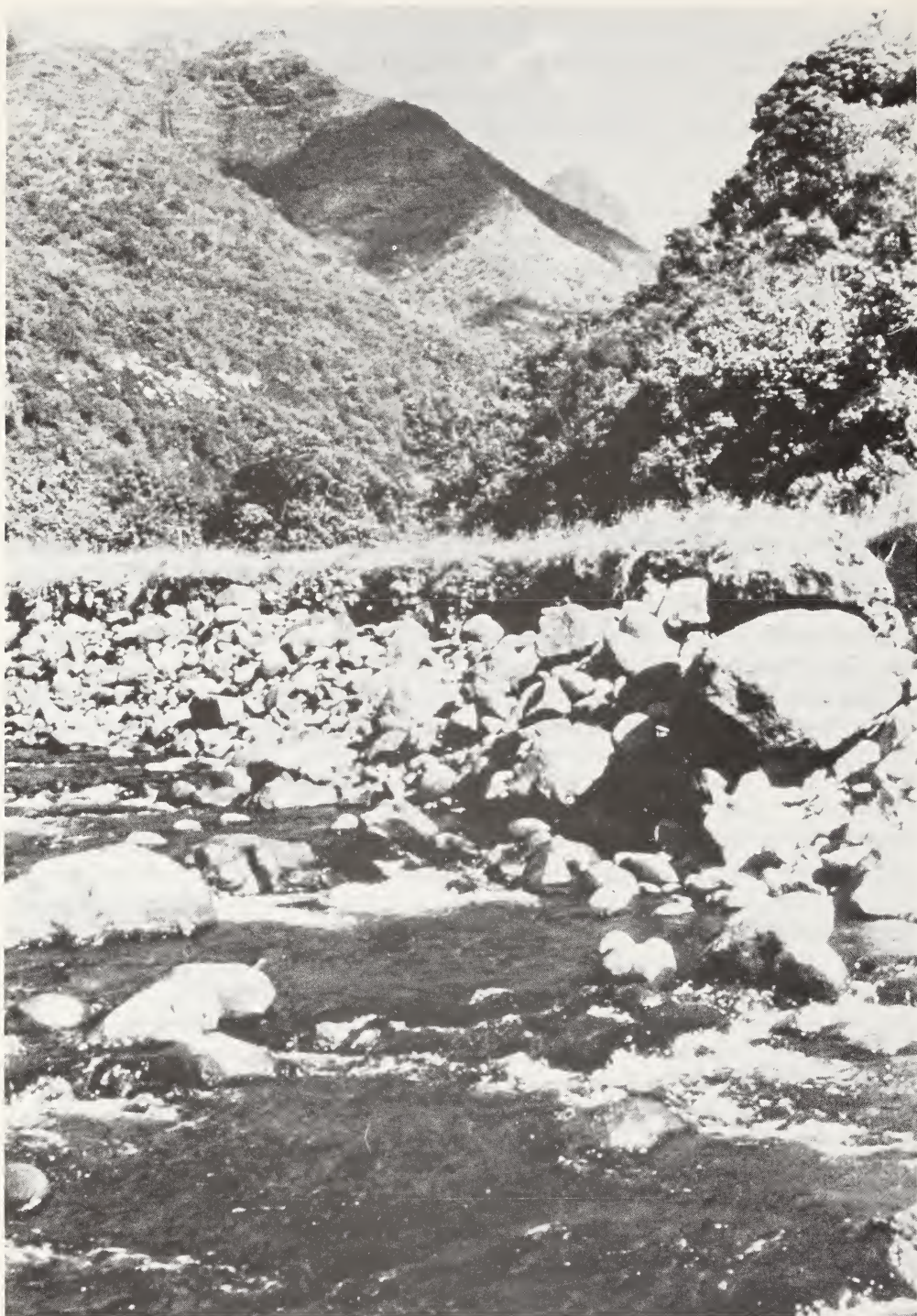
Frontispiece. Tuauru River, Mahina, Tahiti. A typical habitat of larvae of *Simulium tahitiense* Edwards and *S. oviceps* Edwards.

A TAXONOMIC ACCOUNT OF THE BLACK FLIES (DIPTERA: SIMULIIDAE) OF THE SOCIETY ISLANDS - TAHITI, MOOREA AND RAIATEA

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ABSTRACT

The taxonomy of black flies of the Society Islands - Tahiti, Moorea and Raiatea is revised. With the exception of one new species, Simulium anatolicum *n. sp., subgenus* Hebridosimulium *Grenier and Rageau, all species are assigned to the subgenus* Inseliellum *Rubtsov, for which a diagnosis is given. An amended diagnosis is provided for* Hebridosimulium. *Thirteen species are recognised in the Society Islands, of which eight (*S. admixtum *n. sp.,* S. arlecchinum *n. sp.,* S. cataractarum *n. sp.,* S. exasperans *n. sp.,* S. lotii *n. sp.,* S. malardei *n. sp.,* S. mesodontium *n. sp.,* S. neoviceps *n. sp.) are described as new from Tahiti, one (*S. opunohuense *n. sp.) from Moorea, and one (*S. castaneum *n. sp.) from Raiatea. The three previously described species (*S. tahitiense *Edw.,* S. oviceps *Edw. and* S. cheesmanae *Edw.) are fully redescribed. Four species groups are recognised. The* malardei *- group contains* S. malardei, *and* S. teruamanga *Craig and Craig from Rarotonga; the* opunohuense *- group contains* S. lotii *and* S. opunohuense; *the* oviceps *- group contains* S. admixtum, S. arlecchinum, S. castaneum, S. cataractarum, S. mesodontium, S. neoviceps, S. oviceps *and* Simulium sp. *The* tahitiense *- group contains* S. exasperans, S. tahitiense *and* Simulium *"IIS". The other species are left ungrouped. Keys are provided for known larvae, pupae and adults of the Tahitian Simuliidae. Brief information is given on habitats.*

RÉSUMÉ

Une révision de la taxonomie des mouches noires des Îles Société - Tahiti, Moorea et Raiatea est présentée. À l'exception d'une nouvelle espèce, Simulium anatolicum *n. sp., sous-genre* Hebridosimulium *Grenier et Rageau, toutes les espèces sont regroupées dans le sous-genre* Inseliellum *Rubtsov. Une diagnose est produite pour le sous-genre* Inseliellum, *et une diagnose révisée est présentée pour* Hebridosimulium. *Treize espèces sont reconnues pour les îles Société: dont huit nouvelles espèces (*S. admixtum *n. sp.,* S. arlecchinum *n. sp.,* S. cataractarum *n. sp.,* S. exasperans *n. sp.,* S. lotii *n. sp.,* S. malardei *n. sp.,* S. mesodontium *n. sp.,* S. neoviceps *n. sp.) décrites pour Tahiti, une (*S. opunohuense *n. sp.) pour Moorea, et une (*S. castaneum *n. sp.) pour Raiatea. Les trois espèces restantes (*S. tahitiense *Edw.,* S. oviceps *Edw. et* S. cheesmanae *Edw.) sont entièrement redécrites. Quatre groupe-espèces sont reconnus. Le groupe-*malardei *contenant* S. malardei *et* S. teruamanga *Craig et Craig, de Rarotonga; le groupe-*opunohuense *(*S. lotii *et* S. opunohuense*); le groupe-*oviceps *(*S. admixtum, S. arlecchinum, S. castaneum, S. cataractarum, S. mesodontium, S. neoviceps, S. oviceps *et* Simulium sp*), et la groupe-*tahitiense *contenant* S. exasperans, S. tahitiense *et* Simulium *"IS". Les espèces restantes demeurent non-groupées. Des clefs d'identification sont présentées pour les larves, nymphes et adultes connus pour Tahiti. Les habitats sont brièvement décrits.*

INTRODUCTION

Simuliidae occur on many of the world's volcanic and continental islands (Crosskey, 1981). With few exceptions, such as large islands like New Zealand and New Guinea (Smart and Clifford, 1965; Dumbleton, 1973b; McLea and Lambert, 1983), the number of simuliid species

living on individual islands is low. Even for an ecologically diverse and geologically old island such as New Caledonia (Holloway, 1979) only two taxa of simuliids are known, despite moderately intensive collection (Bedo, 1977; 1984).

When simuliids were first reported from Polynesian islands, few taxa were recognized (Edwards, 1927; 1933; 1935) and the taxonomic situation was not definite as Edwards (1927) indicated by comments about *S. cheesmanae*.

While larvae of the Tahitian *S. tahitiense* and *S. oviceps* were common and relatively well described, larvae of *S. cheesmanae* were unknown. Grenier and Rageau (1960) provided more extensive descriptions for *S. tahitiense* and *S. oviceps*, as well as descriptions of new larval and pupal material, suggesting that it might be that of *S. cheesmanae*; but still a relatively simple taxonomic situation.

While studying the number of larval instars of *S. tahitiense* and *S. oviceps* (Craig, 1975a), I too, described new larval material, but realized it was probably not that of *S. cheesmanae* because of its small size, since *S. cheesmanae* is the largest Tahitian simuliid. At that time I also collected larval material for karyotyping. Rothfels *(in* Craig, 1975a) commented that *S. tahitiense* and *S. oviceps* were remarkably close to each other chromosomally. A reconstructed phylogeny of the Tahitian Simuliidae then seemed very simple (Craig, 1975b). Rothfels (pers. comm., 1974) subsequently collected more material himself which included at least one taxon not related to those then known.

In 1980, 1981 and 1983, I collected other species of simuliid in Tahiti which were confirmed karyologically by Rothfels (*in* Craig, 1983) and it became apparent that the Rarotongan, Marquesan and Tahitian species were unique in the Simuliidae by possessing heterogametic females. The taxonomic situation then became far from simple. As can be seen by this present work, many of the new species are morphologically distinct in the immature stages, and an intriguing question is why were they not discovered sooner? In retrospect, two aspects of work on Tahitian Simuliidae provide the answer. Firstly, both *S. tahitiense* and *S. oviceps* larvae prefer the abundant larger, open rivers of Tahiti, while the newly discovered species are in more specialized habitats, such as cascades, small heavily-shaded streams, or from the only lake-fed river on the island. Earlier collections, as judged from locality labels, were simply made from the large rivers which had easier access and probably provided more satisfying results in terms of numbers of specimens. The new species sometimes occur in very low densities, and several are known, unfortunately, only from unique specimens. Secondly, *S. tahitiense* is morphologically variable and the limits of the variation were not then well known. Consequently, *S. exasperans*, *S. lotii* and *S. malardei* had been collected previously by earlier workers and me, but were not recognized.

One of the major difficulties with Tahitian Simuliidae has been association of life stages. Larvae of most species (both karyotyped and not) are morphologically quite distinct, with pupae less so and the adults difficult to distinguish without detailed preparation of their genitalia. Therefore, great care was taken to ensure that adults reared from pupae were correctly associated to their larvae. With as many as four species occurring sympatrically, and with little to distinguish some of the later stages, it is remarkable that the original association of stages of *S. tahitiense* and *S. oviceps* was correct. In large part that was because material taken over the years was from large populations from preferred habitats of those species. However, the probability of *S. tahitiense* being confused with *S. exasperans* n. sp. existed because that species is so similar to *S. tahitiense* and it occurs in the same habitats, at quite high frequency in many places. Likewise, pupae of *S. lotii* n. sp. are easily confused with small pupae of *S.*

exasperans. This raises a serious problem with collections of pinned adults of Tahitian simuliids. Many such specimens are severely collapsed because the adults are small and cannot withstand drying. Therefore many exterior characters cannot be easily seen. Without associated pupal exuviae, and without detailed preparation of the genitalia, specific identification of such pinned adults is almost impossible. This particularly applies to *S. tahitiense* and *S. exasperans*. Indeed, in some collections of pinned reared adults, associated pupal exuviae show that *S. exasperans* had previously been identified as *S. tahitiense*. Consequently the work of correctly identifying present collections of pinned material will be onerous, if not impossible. This makes reared material valuable, and such is essential for future collections.

Of considerable importance for correct association were specimens undergoing larval/pupal moults, which allowed characters of both stages to be definitively associated. A few pupal exuviae from reared adults retained the larval exuviae and these specimens assumed even more importance.

Some larval material which is karyologically distinct cannot yet be morphologically characterized. Rothfels (*in* Craig, 1983) showed two distinct cytotypes, "IIS" and "IS-complex", however, the larval remains from the karyological examination are not adequate to provide sufficient morphological details to erect species for these distinct cytotypes. Larvae of "IIS" are presently morphologically indistinguishable from *S. tahitiense* and those of "IS-complex" cannot be distinguished from *S. cataractarum*.

Interpretation of the type status of previously described species has been difficult because Edwards failed to label his type specimens. It was necessary to infer the types and the status from data labels on the material in the British Museum (Natural History); the lectotypes designated here are from series of syntype specimens so determined by R.W. Crosskey (BMNH). For *S. oviceps*, no Tahitian data were explicitly given for any specimen and syntype status was inferred by Crosskey from Mumford and Adamson's locality data and by back reference to material originally mistakenly identified as *S. bussoni* (Edwards, 1927).

In comparison to Northern Hemisphere simuliids, little is known about the biology of the simuliids from the Society Islands, but Schröder (1985, 1988) has made an important contribution by studying larval distribution, habitats and feeding behaviour.

MATERIAL

More than 200 adults were reared from pupae for this study and a similar number of pinned adults from various institutions were also examined. Approximately 250 larvae were identified to species, but many hundreds of larvae of the commoner species were available.

Codens for institutions where material is deposited:

BMNH   Department of Entomology, British Museum (Natural History), Cromwell
        Road, London, SW7 5BD England.
BPBM   Bernice P. Bishop Museum, P. B. 19000-A, Honolulu, Hawaii, 96819.
        U. S. A.
CNCI   Canadian National Collection of Insects, Arachnids and Nematodes,
        Biosystematics Research Centre, Ottawa, Canada. K1A 0C6.
DAC   Personal collection. D. A. Craig, Department of Entomology, University of
        Alberta, Edmonton, Canada. T6G 2E3.

DSIR   New Zealand Arthropod Collection, Entomology Division, DSIR, Private
        Bag, Auckland, New Zealand.
IP   Institut Pasteur, 25 et 28, Rue du Docteur-Roux, 75724 Paris, France.
MNHP   Department d'Entomologie, Muséum National d'Histoire Naturelle, 45
        Rue de Buffon, 75005, Paris, France.
UASM   Strickland Museum, Department of Entomology, University of Alberta,
        Edmonton, Canada. T6G 2E3.
USNM   United States National Museum, NHB 168, Washington, D. C. 20560,
        U. S. A.

METHODS

Collection and Treatment of Specimens

When possible, two collections of larvae were made, one into Carnoy's fixative for eventual karyological examination, the other into 90% ethanol to extrude the anal papillae. For scarce material, fixation in Carnoy's took precedence.

Adults were reared from pupae placed in tubes with damp filter paper. After emergence, adults were allowed to mature before preservation in 90% ethanol along with their pupal exuviae. Most of this material was critical point dried. Although colours are slightly muted, this is a preferred technique for it results in minimal collapsing. Most museum collections of pinned specimens of Polynesian simuliid adults, which were allowed to dry naturally, collapsed and are of little taxonomic use.

Larvae and pharate pupae for examination by light microscopy were dealt with following Currie (1986). Cleared material was placed in glycerine-jelly as a temporary mountant during examination. Material for scanning electron microscopy was prepared according to Craig and Borkent (1980).

Notes about Structural Features

Determination of homologous hypostomal teeth is not without difficulty when all the teeth are similar in shape and length as in *S. oviceps*, or when only the median tooth is differentiated as in *S. lotii*. Following Currie (1986), I distinguish between apical teeth formed from the dorsal wall of the hypostoma and the lateral serrations formed from the ventral one. For most hypostoma a distinct line marks the two structures (Figs. 36, 37, 39, 40). A prominent apical tooth in a lateral position is termed "lateral tooth - 1 tth", *e.g.,* as in *S. malardei*. Such a decision results in three lateral teeth and two paralateral teeth per side (Fig. 40).

Of particular importance taxonomically is presence or absence of thoracic tubercles on the pupae. When only late last instar larval material is available, with care, some of the pharate pupal cuticle can be dissected out with the pupal gills. Tubercles can then clearly be seen with phase microscopy (Fig. 73). In many older preserved specimens, larval cuticle has separated from the underlying pharate pupa and is relatively easy to remove. The pharate pupal carcass can then be examined with a scanning electron microscope (Fig. 72).

Adult Tahitian Simuliidae are relatively difficult to identify and normally require detailed preparation of their genitalia.

Water Characteristics

To determine amount of suspended material larger than 0.45 μm in the water (Lacey and Lacey, 1983), 500–1000 ml of water were filtered through previously weighed Millipore®, Type
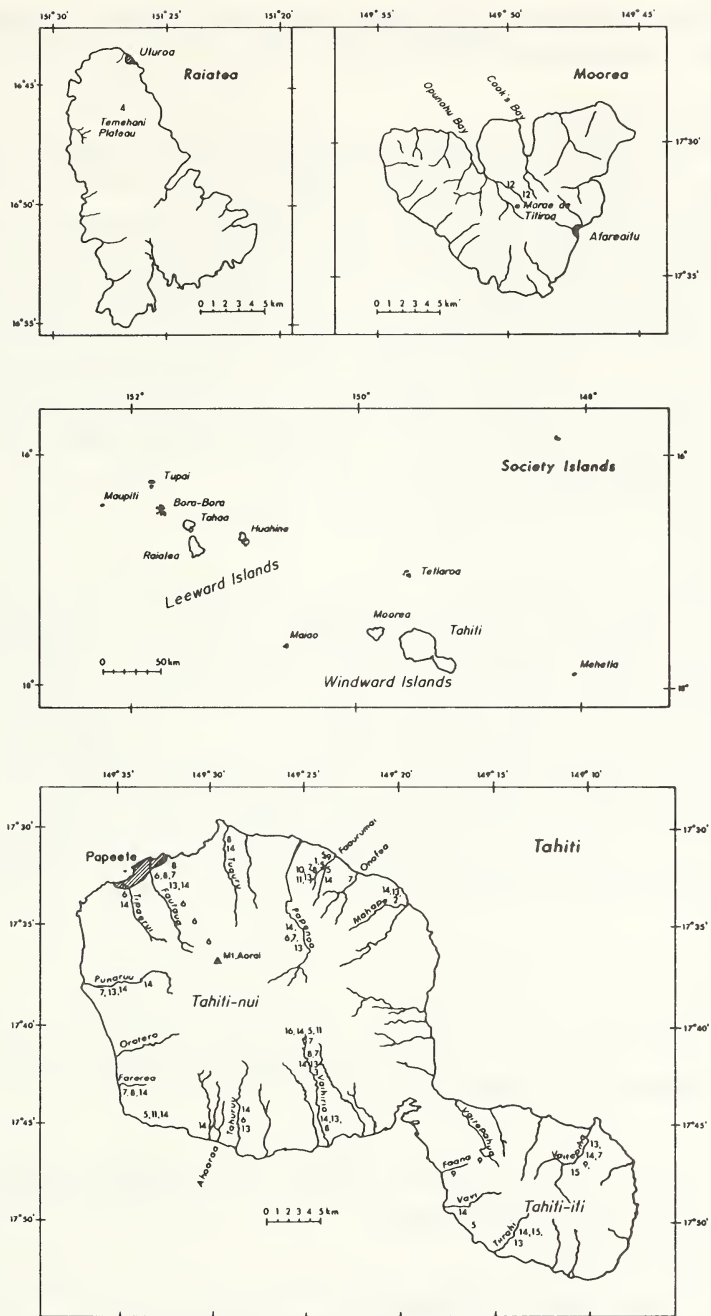
Map 1. Localities and distribution of Black Flies in the Society Islands. 1 = *Simulium admixtum* n. sp.; 2 = *S. anatolicum* n. sp.; 3 = *S. arlecchinum* n. sp.; 4 = *S. castaneum* n. sp.; 5 = *S. cataractarum* n. sp.; 6 = *S. cheesmanae* Edwards; 7 = *S. exasperans* n. sp.; 8 = *S. lotii* n. sp.; 9 = *S. malardei* n. sp.; 10 = *S. mesodontium* n. sp.; 11 = *S. neoviceps* n. sp.; 12 = *S. opunohuense* n. sp.; 13 = *S. tahitiense* Edwards; 14 = *S. oviceps* Edwards; 15 = *Simulium* "IIS"; 16 = *Simulium* sp.

HA filters. These were then dried and reweighed. The pH of water was determined with a portable, Fisher, Digital pH meter, Model 609.

Localities and Locality Data

Polynesian place names are used for most localities. Where alternative spellings are available, both are given initially. Localities are listed in order from Papeete clockwise (*i.e.,* north, east; Map 1) with the district given first and italicized. Tahiti is formed from two extinct volcanic centres, with the larger western land mass termed "Tahiti-nui", the smaller, "Tahiti-iti". Localities on Tahiti-iti are so indicated. Names, longitudes and latitudes were taken from the maps - "Edition Provisoire 1958, 1:40,000, Ministere des Travaux publics et des Transports, Institut Geographique National, France" and "Carte Touristique, 1:100,000, Edition 3, 1977, Institut Geographique National, France". Where distances from the coast, or other definitive statement is made on older collections, longitude and latitude was determined for those localities. Data for a given locality are listed chronologically. Where detailed localities are not given on labels, these are listed first under "*Tahiti*". The station numbers (*e.g.,* Stat. #3) given on some labels refer to data in the author's field notes.

Species Criteria

Possession of a unique character state, or unique combination of character states, was taken as an indication of reproductive isolation and specific status. In most instances, morphological specific status agrees with cytospecies determined by Rothfels (*in* Craig, 1983). Choice of types for three species was dictated by existence of syntypes. Otherwise, the life stage most likely to be encountered and most easily identified was chosen. Larvae were the preferred stage for types because of relative ease of identification. Whenever possible, karyotyped larval material (Rothfels *in* Craig, 1983) has been deposited in the institution holding the type.

Data from labels of type specimens are cited in the manner following O'Hara (1983). Labels are listed from the top down, with each label enclosed in quotation marks; lines of text within a label are indicated by a slash mark. Repositories for all types and material examined are given in parentheses.

Species Groups

Species which appear to be morphologically closely related have been assigned to species groups. At present these are based mainly on pupal and larval characteristics. Some species, such as *S. cheesmanae* for which only adults are known, are not placed in any group.

Figures

In Figures 26–35 of larval head capsules, rays of labral fans have been omitted for clarity, as have the hypostomal sensilla in Figures 36–44.

TAXONOMIC TREATMENT

Key to Female Adults of Tahitian Simuliidae

Use of this key requires preparation of the adults' genitalia. Females of *S. admixtum, S. arlecchinum, S. malardei, S. mesodontium* and *S. neoviceps* are unknown.

1   Large-sized species: body length 2.5–3.8 mm; antennae and legs distinctly
           yellow . . . . .5.

1′   Moderate to smaller-sized species: body length 1.2–2.1 mm; antennae yellow basally; legs dark, or with yellow/pale pattern 2

2 (1′) Body: blackish-brown; length 1.2–1.6 mm 3

2′   Body: brownish; length 1.5–1.9 mm 4

3 (2) Body: black. Genitalia: cerci and anal lobe small; lateral sclerite of genital fork simple; sternite VIII with median pigmented region ovoid (Fig. 6) . . .
    . . . . *S. lotii* n. sp., p. 388

3′   Body: brownish-black. Genitalia: cerci and anal lobe large; lateral sclerite of genital fork with accessory arm; sternite VIII with median pigmented region broad and diffuse (Fig. 8) . . . . *S. oviceps* Edwards, p. 405

4 (2′) Genitalia: spermatheca without reticulate pattern; lateral sclerite of genital fork with anterior projection sharply rounded (Figs. 5, 9) 6

4′   Genitalia: spermatheca with slight reticulate pattern; lateral sclerite of genital fork with anterior projection blunt (Fig. 3) . . . .
    . . . . *S. cataractarum* n. sp., p. 400

5 (1) Calcipala: expanded enormously. Anepisternal membrane: haired *(Hebridosimulium)*. Genitalia: cerci narrow basally and apically; hypogynial valves locked basally to anal lobes; sternite VIII with median pigmented region deeply concave (Fig. 1) . . . . . *S. anatolicum* n. sp., p. 382

5′   Calcipala: not so expanded. Anepisternal membrane: bare *(Inseliellum)*. Genitalia: cerci broadly rounded apically; hypogynial valves free of anal lobe bases; sternite VIII with pigmented region diffuse, subrectangular medially (Fig. 4) . . . . *S. cheesmanae* Edwards, p. 385

6 (4) Sternite VIII: with median pigmented region small; genital fork stem broader; anal lobes bare (Fig. 5) . . . . *S. exasperans* n. sp., p. 392

6′   Sternite VIII: with median pigmented region distinct, extended laterally; genital fork stem slim; anal lobes hairy (Fig. 9) . . . .
    . . . . *S. tahitiense* Edwards, p. 394

Key to Male Adults of Tahitian Simuliidae

Use of this key requires preparation of the adults' genitalia. Males of *S. admixtum*, *S. arlecchinum*, *S. mesodontium* and *S. neoviceps* are unknown.

1   Large-sized species; body length 3.0 mm (Fig. 11) . . . .
    . . . . *S. cheesmanae* Edwards p. 385

1′   Moderate to small-sized species; body length less than 2.5 mm 2

2 (1′) Gonocoxa: median surface straight to slightly concave, no medial projection (Figs. 10–16) 3

2′   Gonocoxa: median surface convex, with medial projection (Fig. 17) . . . . .
    . . . . *Simulium* sp. p. 408

3 (2) Small-sized species; body length less than 1.5 mm 4

3′   Moderate-sized species; body length between 1.6–2.5 mm 5

4 (3) Ventral plate: heart-shaped; bare; anterior arms subparallel to curving medially; anteriomedian notch indistinct (Fig. 14) . . . .
    . . . . *S. malardei* n. sp., p. 387

4′   Ventral plate: broad; posteromedian region hairy; anterior arms diverging; anterior median notch rounded, distinct (Fig. 15) . . . .

.... *S. oviceps* Edwards, p. 405

5   (3′)   Ventral plate: broadly rounded anteromedially; median notch broad (Figs.
              10, 12, 16) 6

5′   Ventral plate: protruded anteriorly; median notch deeply incised (Fig. 13)
              ....*S. lotii* n. sp., p. 388

6   (5)   Ventral plate: anterolateral arms flanged distally (Figs. 10, 12) 7

6′   Ventral plate: anterolateral arms smooth distally (Fig. 16) ....
              .... *S. tahitiense* Edwards, p. 394

7   (6)   Ventral plate: posterolateral margins concave distally, cone-shaped, hairy
              medially ....*S. exasperans* n. sp., p. 392

7′   Ventral plate: posterolateral margins slightly concave, posterior apex
              broad, hairy posteriorly ....*S. cataractarum* n. sp., p. 400

Key to Pupae of Tahitian Simuliidae

Pupae of *S. admixtum*, *S. cheesmanae* and *S. neoviceps* are unknown.

1   Thoracic tubercles: present (Fig. 18); pupal cocoon: either boot- or
              slipper-shaped 2

1′   Thoracic tubercles: absent (Fig. 19); pupal cocoon: slipper-shaped 3

2   (1)   Gill filaments: shorter than thorax; postscutellum not cone-shaped in
              lateral view (Fig. 18); cocoon boot-shaped ....*S. anatolicum* n. sp., p. 382

2′   Gill filaments: as long or longer than thorax; postscutellum cone-shaped in
              lateral view (Figs. 20, 21); cocoon slipper-shaped 4

3   (1′)   Dorsal gill filament: shorter than other filaments .. *S. lotii* n. sp., (p. 388)
              and *S. cataractarum* n. sp., (p. 400) ....5.

3′   Dorsal gill filament: as long as other filaments ....,.........
              .... *S. exasperans* n. sp., p. 392 and *S. malardei* n. sp., p. 387

4   (2′)   Thoracic tubercles: rounded; dorsal gill filament longer than thorax,
              sometimes reflexed posteriorly (Fig. 21) .... *S. tahitiense* Edwards, p. 394

4′   Thoracic tubercles: pointed; dorsal gill filament shorter than thorax and
              other filaments, rarely long (Fig. 20) .... *S. oviceps* Edwards, p. 405

5   (3)   Pharate pupal material indicates that *S. arlecchinum* n. sp.. (p. 398) and *S.
              mesodontium* n. sp., (p. 403) may also have short dorsal gill filaments and
              lack thoracic tubercles.

Key to Mature Late Instar Larvae of Tahitian Simuliidae

The larvae of *S. cheesmanae* and *S. anatolicum* are unknown.

1   Labral fan: fully developed; head spot pattern positive (Fig. 35). Posterior
              abdomen: expanded gradually (Fig. 22), or expanded ventrally (Fig. 23).
              Anal sclerite extended laterally 7

1′   Labral fan: rays reduced in number or size, or virtually absent (Figs. 32,
              34, 66, 67); head spot pattern partially (Figs. 28, 32), or completely
              negative (Figs. 29, 34). Posterior abdomen: hemispherical, or abruptly
              expanded laterally at segment VI (Fig. 25). Anal sclerite extended
              laterally, or almost, or completely extended around anal proleg (Fig. 24)

Subgenus *Hebridosimulium* Grenier and Rageau

Hebridosimulium Grenier and Rageau, 1961a: 96 (as genus). Type species: *Simulium jolyi* Roubaud, 1906 (by original designation).

Simulium (Hebridosimulium) Grenier and Rageau. Crosskey, 1967: 27.

Diagnosis.-— As for Crosskey (1967), but with the following modifications necessitated by additional material from Fiji and Vanuatu and by present description of a new species from Polynesia. Adult: with or without distinct "cell" basal to anterior branch of media (MA); cibarial pump without armature; hypogynial valves and anal lobes coadapted basally; spermatheca with slight or heavy pattern, with or without clear area around junction of sperm duct.

Pupa: dorsal thoracic tubercles rounded, lateral and posterior tubercles pointed; gill with eight or ten simple elongated filaments; scutellum not pointed dorsally.

Simulium (Hebridosimulium) anatolicum n. sp.
(Figs. 1, 18, 69)

Types.—

Holotype. Female: pinned; reared, with pupal cocoon and exuviae as subsidiary material; label data:- "Holotype", "Simulium (H.)/ anatolicum Craig/ det./ D.A. Craig 1986", "Tahiti, Mahaena, Mahape R./ 17° 34 ' 00" S. 149° 20 ' 33" W./ alt. 700m. 14-vi-1980,/ D.A. & R.E.G. Craig. Stat. #6." (MNHP). Head, genitalia and pupal exuviae in vial. Left gill of pupa as slide mount, same data as adult (MNHP). Small portion of pupal exuviae used for scanning electron microscopical examination (DAC).

Specific epithet.— The specific epithet is based on the Greek word "anatolios", meaning "eastern", in reference to this new record well to the east of other *Hebridosimulium*.

Diagnosis.—

Adult: large; yellowish; mandibles small; wing with no basal "cell", veins R1, Sc, lacking hair; spermatheca, pattern tuberculate, unpigmented region at junction of sperm duct.

Pupa: sternite V hooks close-set.

Description.—

Adult female. (Single reared specimen). Body: generally yellowish-brown. Length: 2.5 mm. Head: grayish-brown, width 0.98 mm, length 0.69 mm. Eyes: yellowish-grey; interocular distance 0.33 width of clypeus; frontal angle, 115 degrees; ommatidia 0.014 mm in diameter, *ca.* 34 and 45 respectively across and up eye in middle row. Frons: bulging ventrally over sunken antennal bases, densely covered with silver scale-like hairs. Clypeus: concolorous with ventral region of frons, slightly longer than wide, densely covered with silver hairs medially; lateral hairs dark, extended beyond bases of maxillary palpi. Postocciput: densely covered with silver hairs extended to eye margin, scattered long black hairs extend over posterior margin of eye. Antenna: yellowish; length 0.63 mm. Mouthparts: length, 0.50 head depth; mandibles with *ca.* 30 very fine teeth; lacinia with *ca.* 25 pronounced retrorse teeth; maxillary palpus (distal articles absent from specimen), basal articles flattened and densely covered with black hairs; sensory vesicle of third article elongated occupying 0.50 width of article, opening of vesicle 0.66 width of vesicle, *ca.* 25 bases of sensilla visible. Cibarial pump: space between proximal arms flat, smooth, 1.3 times as wide as deep. Thorax: rich brown; length 1.4 mm; postpronotum, contiguous area with scutum creamy, remainder of scutum uniformly brown, moderate vestiture of silver hair, in some views three darker vittae; scutellum yellowish, with sparse black and golden hairs; postnotum brown medially and posteriorly, yellow laterally; anepisternal membrane with distinct pale yellow flattened hairs; katepisternum bare; mesepimeral hair tuft black, sparse. Wing: length 2.9 mm, maximum width 1.3 mm; veins pale yellow, hairs black; stem vein hair tuft black, covering vein; basal section of vein R with hairs dorsally and ventrally; R1 clear dorsally; Sc clear dorsally, with hairs ventrally; area basal to vein MA without distinct clear "cell". Halter: creamy-white. Legs: coxae, femura and tibiae yellow, distal portion of tibiae brown; fore basitarsus six times longer than wide, brown anteriorly; hind basitarsus parallel sided, seven times longer than wide; calcipala enormously extended to 0.66 length of 2nd tarsomere; 3rd tarsomere with two long hairs extended to pretarsal claws. Pretarsal claw: smoothly curved, simple, no basal tooth. Abdomen: generally black with dense dark scales anteriorly, pale scales posteriorly on each segment; basal fringe of shiny dark golden hairs extended to abdominal segment II; tergites III–VII lighter in colour than others; sternite VII distinct, narrower anteriorly; pleural regions with dense silver scales. Genitalia (Fig. 1): complex; cercus, sharply ovoid distally in ventral view; anal lobes straight sided medially, almost in contact under hypogynial valves, divergent posteriorly almost at right angles; valves divergent only slightly posteriorly, closest approach before apex, bluntly rounded posteriorly; sternite VIII with posterolateral edges of valves very thin; bases of valves and anal lobes interlock, with anterolateral edge of anal lobe overlapping ventrally base of valve; genital fork stem smooth, thin, with slight anterior knob, lateral arms divergent at right angles, lateral sclerite acutely triangular. Spermatheca (destroyed during preparation for illustration): dark brown; distinct turberculate pattern; region at duct junction unpigmented.

Adult male. Unknown.

Pupa. Length; 3.6 mm. Gill (Fig. 18): 1.4 mm in length, eight filaments, branching directly out of base; two ventral filaments branching from short stem, single median filament directed anterolaterally from base; dorsal branch dividing into three, two of these divide again, medial filament single. Head and thoracic cuticle (Fig. 69): with rounded black tubercles, those more lateral and posterior, pointed and hooked. Thorax: trichomes trifid. Abdomen: tergite II with spine combs anteriorly; tergites III and IV with eight recurved hooks posteriorly; last tergite small, with spine field anteriorly;

caudal sclerite with distinct terminal spines; sternites V and VI each with six hooks. Cocoon: boot-shaped, 4.6 mm long, 1.6 mm wide, 1.9 mm high; length of ventral lip 1.9 mm; opened at 45 degrees to base, lateral and posterodorsal edges well formed, anteroventral edge rough, with small fenestrae.

Larvae. Unknown.

Bionomics.— The pupa from which the adult was reared came from grass trailing in a small, rapidly flowing, open stream. Velocity was *ca.* 80 cm/s and temperature 29° C. *Simulium tahitiense* and *S. lotii* were taken from the same locality.

Distribution.— The subgenus *Hebridosimulium* was previously known only from Fiji and Vanuatu (=New Hebrides), where it is widely distributed. This new record from Tahiti, represents a range extension of some 3500 km.

Phylogenetic Relationships.— Dumbleton considered the simuliid from Fiji to represent a species separate from *S. jolyi* of Vanuatu (=New Hebrides). Crosskey (1974), on the other hand, maintained that *S. laciniatum* and *S. jolyi* were conspecific subspecies.

Since the morphological character state differences between adults and pupae of the taxa in *Hebridosimulium* are of the same nature as those which separate species within *Inseliellum* and which are corroborated karyologically (Rothfels *in* Craig, 1983), it seems logical to consider the three taxa in *Hebridosimulium* as species. Further, the great distances between the respective islands and likely lack of vicariant genetic interchange among their simuliid faunas for considerable time (*e.g.,* maximum six to 13 million years between Fiji and Vanuatu. Doutch, 1981), adds weight to the probable specific status of these taxa. For the present, I hypothesize specific status for the Tahitian *Hebridosimulium*.

The discovery of a single specimen from a subgenus unexpected in Tahiti initially suggested that it was a contaminant from collections made either in Fiji or Vanuatu. However, *S. anatolicum* is morphologically distinct from *S. jolyi* and *S. laciniatum*. The pupa of *S. anatolicum* has only eight filaments, not ten, indicating that perhaps it is more closely related to the Fijian *S. laciniatum*. Further material from Tahiti, and detailed karyological and morphological examination of extensive collections in my possession from both Fiji and Vanuatu may help resolve this situation.

Rothfels (pers comm., 1986), commented that *S. anatolicum* might be the cytospecies he had found on Tahiti and termed "forbidden" (*in* Craig, 1983). Apparently "forbidden" and *Hebridosimulium* had similar karyological characteristics.

Subgenus *Inseliellum* Rubtsov

Inseliellum Rubtsov, 1974: 275 (as genus). Type species: *Simulium oviceps* Edwards 1933, by original designation and monotypy (see Crosskey, 1987 for discussion).
Simulium (Inseliellum) Rubtsov. Craig and Craig, 1986: 357. Crosskey, 1987: 388.

Rubtsov (1974) did not provide a diagnosis for *Inseliellum* beyond stating that the characteristics were as given for *S. oviceps* by Grenier and Rageau (1960: 734–735). Since Craig (1975a, b; 1977; 1983), Crosskey (1987), and this work, show fairly conclusively that *Inseliellum* is not just restricted to *S. oviceps*, a more detailed diagnosis is provided.

Diagnosis.—

Adult Female. Cibarial pump: unarmed. Wing: basal section of radius haired. Thorax: scutum without conspicuous pattern; pleural membrane bare; katepisternum bare. Legs: fore tarsus slender, fore basitarsus five to seven times as long as its greatest width; calcipala, extended to 0.50 length of adjacent tarsomere; pedisulcus not prominent; claws with large basal tooth. Abdomen: covered with pale scales, semishining or dull on last few segments; sternite VII clearly developed. Genitalia: hypogynial valves rounded or slightly angulate apically in lateral

view; anal lobes normal; cerci rounded to angulate; spermatheca with faint pattern, clear area at junction of sperm duct. Heterogametic.

Description.—

Adult Male. Upper eye: ommatidia not exceptionally enlarged, 12–22 rows. Thorax: scutum without bold pattern. Legs: hind basitarsus slightly dilated. Genitalia: gonostyles simple, tapered, with single substantial terminal spine; ventral plate not toothed, broadly subtriangular, with moderately well developed shoulders, basal arms short, directed anteriorly, rounded or angular; median sclerite simple, rod-shape; parameres long and slender.

Pupa. Gill: shorter than, or as long as, pupa; four to eight fine filaments, dorsal filaments variable, shorter than, or as long as others. Thorax: tubercles present or absent, rounded or pointed; trichomes simple; scutellum pointed or rounded dorsally. Abdomen: onchotaxy normal; tergites I and V bare, II–IV with hooks, VI–VIII with spine combs; terminal spines small to absent. Cocoon: slipper-shaped.

Larva. Head: margins from essentially parallel to strongly convex; antenna either shorter than labral fan stem or just longer; labral fans normal to strikingly reduced, rays variable, from normal numbers and shape, to reduced in number, and/or reduced in size to essentially absent; spot pattern ranging from positive to negative; frontoclypeal apotome variable in shape, from wide posteriorly, to narrow; apotome cuticle variable, ranging from normally smooth to strongly corrugated, and/or with raised sensillar sockets; sensilla number normal or very numerous; postgenal cleft variable, from broadly rounded to essentially absent; hypostoma variable, ranging from 12–15 apical teeth, with median and lateral teeth prominent and three sublateral teeth per side, or four or five sublateral teeth per side and only median tooth prominent, or no teeth prominent, or median tooth absent; hypostoma produced anteriorly normal amount, to strongly produced, four to eight hypostomal sensilla, normally lying in rows parallel to hypostomal edge, or tightly grouped; mandibles normal, to short and robust, serration various, from subequal sides, to one side half length of other, sides concave or flat, apex sharp; basal sensillum either on base of serration or on mandible. Abdomen: posterodorsal cuticle with small trichoid, bifid, trifid, or stellate sensilla; cuticle either smooth, tuberculate or with laterally elongate ovoid, low tubercles; general shape either normal, gradually increased and decreased in size, broadcast at segment VI or VII. or expanded abruptly ventrally at segment VI and abruptly posteriorly at segment VIII, or expanded abruptly laterally at segment VI and decreased gradually posteriorly; posteroventral tubercles present or absent. Anal papillae complex with secondary papillae, or one or all papillae simple. Rectal scales absent. Posterior circlet of hooks with 60–108 rows of 10–17 hooks.

Bionomics.— Eggs laid on rocks (Craig, 1983), or vegetation (Schröder, pers. comm., 1987). Larvae and pupae found on rocks or vegetation in a great variety of habitats, ranging from large, fast open rivers to small, densely-shaded streams; in trickles of water and in leaf packs on upstream surfaces of rocks (Craig and Craig, 1986).

Geographic Distribution.— Polynesia: Huahine, Marquesas, Moorea, Rarotonga, Raiatea, Tahiti (Craig, 1983; Craig and Craig, 1986; Séchan *in* Klein *et al.*, 1983). Possibly Micronesia: Guam, Palau, Truk (Crosskey, 1987).

Phylogenetic Relationships.— *Inseliellum* morphologically is close to *Eusimulium* and *Pomeroyellum* and is difficult to separate from those taxa. As Grenier and Rageau (1960) indicated, adult characteristics of Tahitian species of *Inseliellum* place it very close to *Eusimulium* Roubards as defined by Edwards. Edwards (1935) commented that the Tahitian and Marquesan simuliids formed a distinct subgroup within *Eusimulium*, but he did not state his basis for that comment. Under a scheme suggested by Freeman and de Mellion (1953), Grenier and Rageau (*loc. cit.*) suggested that the three then known Tahitian species belonged to Division A. Group I, of *Simulium*. They further comment that the Tahitian species cannot be placed in *Eusimulium* as defined (Rubtsov, 1956), because of lack of conical ventral tubercles in the larvae. However, these structures are present, although not as well developed as in *Eusimulium*. Edwards (1932) commented that the difference between typical *Eusimulium* species and Tahitian species is the latter's complete absence of hair on the upper surface of the Rs vein and eight pupal gill filaments. Edwards further noted that in these features they resembled Enderlein's *Gomphostibia*. He was not aware that some of the Marquesan species have the typical *Eusimulium* arrangement of four pupal gill filaments (Séchan *in* Klein *et al.*, 1983). Rubtsov (1974) states that *S. oviceps* and *S. tahitiense* have affinities with *Eusimulium*. Craig (1983) briefly considers the similarity of Polynesian Simuliidae to *Pomeroyellum* and the possibility that ancestral Polynesian simuliids may have entered the

Pacific from the West.

Because of the problem of indistinct morphological limits to the subgenera, the main feature that will probably establish monophyly of *Inseliellum* is karyological *i.e.,* heterogametic females. Establishing the sister taxon to *Inseliellum* for outgroup analysis for cladistic purposes will probably be difficult.

Simulium (Inseliellum) cheesmanae Edwards
(Figs. 4, 11)

Simulium cheesmanae Edwards, 1927: 242. Lectotype female (by present designation), TAHITI. Edwards, 1935: 38.
    Smart, 1945: 502.
Simulium (Inseliellum) cheesmanae Edwards. Crosskey, 1987: 388.

Types.—

Lectotype. Female: pinned. By present designation; label data:- "Lectotype", "Syntype", "Society Is. Tahiti./ 8.3.25. E. Cheesman./ BM 1925-464", "Simulium cheesmanae Edw. SYNTYPE ♀/ det. R.W. Crosskey 1979", "Simulium (I.)/ cheesmanae /det /D.A. Craig 1986" (BMNH). Missing right antenna. Both wings with damaged anterior veins.

Paralectotypes – designated from syntypes. Female: pinned; head and genitalia cleared; in vial; same data as for lectotype, but date "5.5.25" (BMNH). Female: cleared; in vial; same data as for lectotype, but date "10.3.25" (BMNH). Male: cleared; in vial; label data:- "Mataeia Aug 1928 A Tonnoir" (BMNH).

Diagnosis.—

Adult female: large; antennae and legs yellow.

Description.—

Adult Female. Body: generally dark brown; length 2.9–3.8 mm. Head: dark brown, with distinct areas pollinose; width 1.1 mm, depth 0.8 mm. Eyes: interocular distance slightly less than 0.33 width of clypeus; frontal angle, 95 degrees; ommatidia 0.023 mm in diameter, *ca.* 27 and 52 respectively, across and up eye in middle row. Vertex: dark brown ventrally to frons, regions adjacent to eyes silvery-pollinose extended down between antennae; vestiture of sparse golden hairs. Clypeus: as long as wide; silvery-pollinose. Post-ocular hairs: barely extended anteriorly to eye margin. Antenna: length 0.71 mm; dark yellow, lighter basally. Mouthparts: length less than 0.33 head depth; mandibles insubstantial, with only fine apical serrations; lacinia with *ca.* 26 pronounced, pigmented retrorse teeth; palpus, 0.8 mm long, distal article 0.4 mm long; third article with distal medial angle distinct, sensory vesicle occupying 0.33 width of third article, 0.50 width of vesicle, *ca.* 10–14 sensilla sockets barely visible. Cibarial pump: space between proximal arms slightly less than twice as wide as deep, rounded with slight medial projection. Thorax: dark brown to black; length 1.6–1.8 mm; postpronotal lobes distinct with broadly rounded anterolateral margins, slightly pollinose in dorsal view; scutum uniformly very dark brown, faint vittae in some views; scutellum and postnotum concolourous with scutum; scutellum subshiny, with hairs on posterior edge directed anteriorly; postnotum prominent, pollinose in some views; pleuron light brown. Wing: length 3.7–4.2 mm, maximum width 1.4–1.9 mm; basal cross veins dark brown; stem vein yellow, hair tuft black. Halter: yellow. Legs: generally yellow, fore- and meso-tarsi dark brown; metabasitarsus and distal metatarsomere dark brown to black, distal region of metatibia darker; pretarsal claw, smoothly curved with moderately sharp apex, prominent basal tooth slightly longer than 0.50 length of claw. Abdomen: generally dark brown; basal fringe of golden hairs extended to abdominal segment III; tergites I–V with sparse golden hairs, remainder of tergites slightly pollinose under denser golden hairs; pleural and sternal regions greyish. Genitalia (Fig. 4): cercus, blunt apically in ventral view, narrow basally; anal lobe twice as broad as long; hypogynial valves very broad, median edges virtually straight, extended well over anal lobe; genital fork stem smooth and narrow, slightly wider anteriorly; lateral arms broad and smooth, lateral sclerite triangular, anterior apex forming 90°; sternite VIII slightly sclerotized for full width with median rectangular region more heavily sclerotized. Spermatheca: slightly ovoid; heavily pigmented; no reticulate pattern; unpigmented region at junction of sperm duct normal.

Adult Male (Single Specimen). Body: generally brownish-black; length 3.1 mm. Head: width 1.3 mm, depth 0.9 mm. Eyes: upper ommatidia orangey-red; 0.068 mm in diameter, 13 and 15 respectively up and across the eye; lower ommatidia dark brownish-red, 0.025 mm in diameter. Frons: slightly more than 0.33 head width; dark black-brown, slightly pollinose. Clypeus: dark brown; 0.20 as wide as head. Antenna: length 0.7 mm; scape, pedicel and basal portion of first flagellomere yellowish, remainder light brown; first flagellomere as long as scape and pedicel; whole antenna slender in appearance. Mouthparts: very short, 0.16–0.20 as long as head depth; mandibles possibly absent; lacinia without retrorse teeth, apex hairy; palpus 0.69 mm long, apical article 0.35 mm in length, sensory vesicle in third article 0.33 as wide as article, opening

0.33 as wide as vesicle, *ca.* 10 sensilla sockets visible. Cibarial pump: space between proximal arms deeply U-shaped, with smooth edge. Thorax: length 1.1 mm; postpronotal lobe with vestiture of golden scales; scutum uniformly black, vestiture as for postpronotal lobe; scutellum and postscutellum concolourous with scutum; scutellum with sparse black hairs, otherwise bare. Wing: length 2.7 mm, maximum width 1.3 mm. Halter: yellowish. Legs: yellowish-brown; vestiture of dense yellowish-brown hairs; hind leg with femur 3.0 times longer than greatest width, tibia 3.3 times longer than width; pretarsal claw with *ca.* 22 grappling hooks. Abdomen: dark brown with pilose areas; basal fringe of long golden hairs extended to abdominal segment III. Genitalia (Fig. 11): gonocoxa approximately twice as long as maximum width; gonostylus *ca.* 0.33 as wide as long, slightly curved with one blunt terminal spine, slightly longer than wide; ventral plate extensively haired medially, cone-shaped posteriorly, posterolaterally concave, anterior arms concave anteromedially, anteromedian notch broad.

Pupa. Unknown.

Larva. Unknown.

Bionomics.— The females of this species are the largest of the Tahitian simuliids. Although J. L. Gressitt (label data) has taken specimens of *S. cheesmanae* at higher altitudes in Malaise traps, adults are also collected at lower altitudes flying around humans, where the simuliids are very conspicuous because of their colour. The largest specimen ever taken was probing the skin of a man's neck. The substantial teeth on the laciniae indicate that the females may be capable of blood feeding. It is possible that this is the species which gave rise to the intriguing, older reports of Tahitian simuliids feeding on humans (Edwards, 1927; Cheesman, 1932).

Phylogenetic relationships.— Although Grenier and Rageau (1960) suggested that the immature stages of the species named later herein as *S. lotii*, might be those of *S. cheesmanae*, this is clearly not so since all stages of *S. lotii* have been associated. Furthermore, individuals of *S. lotii* are amongst the smallest of Tahitian simuliids. It is interesting that no *S. cheesmanae* adults were obtained from the many pupae reared during this study. Large larvae, distinct from those of *S. tahitiense*, the next largest Tahitian simuliid, have not been found. This suggests that *S. cheesmanae* either occurs at very low frequencies and the adults are concentrated by their host-seeking behaviour around man, or they have an unusual habitat yet to be discovered, or both. The male is assumed to be that of *S. cheesmanae* because of its association with females of that species and because of its large size.

Material Examined.— In addition to types, I have seen the following:

Tahiti. 03-viii-25, L.E. Cheesman (1 ♀, BMNH); 05-viii-25, L.E. Cheesman (1 ♀, BMNH); 00-i-68, J.C. Hitchcock (10 ♀, USNM).

Papeete, Fautaa (sic.) V. alt. 1000', 23-viii-28, A.M. Adamson (1 ♀, BPBM); Fautaua V. alt. 1500', 11-xi-28, A.M. Adamson (1 ♀, BPBM); Mt. Aorai. alt. 4000–5000', 16-ix-34, E.C. Zimmerman (1 ♀, BPBM); Fare Rau Apa. 00-i-60, N.L.H. Krauss (1 ♀, BPBM); Fautaua V. alt. 25 m, 5/11-vii-61, J.L. Gressitt (1 ♀, BPBM); NW. ridge, Mt. Aorai. alt. 1400–1450 m, 10-vii-61, J.L. Gressitt (1 ♀, 1 ♂, BPBM); Fautaua R., Bain Loti. 17° 33' 15" S. 149° 33' 00" W. 08-vii-80, D.A. & R.E.G. Craig (1 ♀, CNCI); Fautaua R., Papeete. 17° 35' 30" S. 149° 31' 42" W. 1-vii-81, D.A. Craig (1 ♀, MNHP).

Faaa, Papearii. alt. 600', 09-xi-28, A.M. Adamson (1 ♀, BPBM); Tipaerui V (= V. de la Reine), 17° 33' 20" S. 149° 25' 45" W. 12-ix-28, A.M. Adamson (1 ♀, BPBM).

Papenoo, Papenoo V. 17° 36' 22" S. 149° 25' 08" W. 25-x-28, A.M. Adamson (1 ♀, BPBM); Papenoo V., 13-ii-61, N.L.H. Krauss (1 ♀, USNM).

Papara, Papara V. (?=Taharuu V), alt. 750', 21-xii-28, A.M. Adamson (1 ♀, BPBM); Mumford & Adamson (1 ♀, BMNH).

malardei - group

Diagnosis.—

Pupa: thoracic tubercles, present or absent, if present rounded.

Larva: hypostomal sublateral teeth, four or less; paralateral teeth, two or more; posterior abdominal segments with dorsal tubercles.

This group may eventually include some of the Marquesan simuliids.

Included taxa.— *Simulium teruamanga* Craig and Craig (Craig and Craig, 1986); RARATONGA: *Simulium malardei* n. sp.; TAHITI.

Simulium (Inseliellum) malardei n. sp.
(Figs. 14, 22, 40, 51, 59)

Simulium "new". Craig, 1983: 534.

Types.—

Holotype. Larva: last instar; in alcohol; label data:- "Holotype", "*S. malardei*", "Tiarei, west of Trou du Souffleur,/ 17° 31' 30" S. 149° 23' 32" W./ alt. 10m, 17-ii-87, D.A. Craig" (MNHP).

Paratypes. Male: reared; pinned; with pupal exuviae and cocoon as subsidiary material; cleared, in vial; label data:- "Paratype", "Simulium (I.)/ malardei Craig/det./ D.A. Craig 1986", "TAHITI, Tahiti-iti, Tautira, /E. trib. Vaitepiha R.,/ 17° 46' 58" S. 149° 10' 39" W./ alt. 50m, 17-ii-83,/ D.A. Craig. Stat. #61" (MNHP). Female: reared; pinned; with pupal exuviae and cocoon as subsidiary material; label data:- as for male (MNHP). Pupa: label data:- "Paratype", "Simulium (I.)/ malardei Craig/ det./ D.A. Craig 1986", "Tahiti-iti, Tautira, E. trib. Vaitepiha R.,/ 17° 46' 30" S. 149° 10' 20" W. alt. 50m,/ 19-vii-80, D.A. Craig." (1, MNHP). Larva: as slide mount; label data:- "Paratype", "Simulium (I.)/ malardei Craig/ det./ D.A. Craig 1986", "Tahiti-iti, Plateau de Taravao, Trib. Vaitepahua R., 17° 46' 25" S. 149° 15' 26" W./ alt. 640m, 10-vii-73," D.A. Craig" (CNCI). Larva: as slide mount; label data:- "Paratype", "Simulium (I.)/ malardei Craig/ det./ D.A. Craig 1986", "Tahiti-iti, Tautira, E. trib. Vaitepiha R.,/ 17° 46' 30" S. 149° 10' 20" W. alt. 50m,/ 19-vii-80, D.A. & R.E.G. Craig. Stat. #12" (BMNH). Larva: last instar; as slide mount; label data:- "Paratype", "Simulium (I.)/ malardei Craig/ det./ D.A. Craig 1986", "Tahiti-iti, Tapuaemaui, Fanaa R.,/ 17° 47' 20" S. 149° 17' 25" W. 15-ii-1984, P. Schröder." (BMNH). Larva: last instar; as slide mount; label data:- "Paratype", "*S. malardei*", "Tahiti-iti, Tautira, E. trib. Vaitepiha R.,/ 17° 46' 58" S. 149° 10' 39" W./ alt. 50m, 02-vii-81,/ D.A. & R.E.G. Craig" (MNHP).

Larvae: in alcohol; label data:- "Paratype", "Simulium (I.)/ malardei Craig/ det./ D.A. Craig 1986", "Tahiti-iti, Plateau de Taravao, Trib. Vaitepahua R.,/ 17° 46' 25" S. 149° 15' 26" W. 10-vii-73,/ alt. 640m, D.A. & R.E.G. Craig" (9, BMNH; 8, MNHP). Larvae: penultimate instar; label data:- "Paratype", "Simulium (I.)/ malardei Craig/ det./ D.A. Craig 1986", "Tahiti-iti, Tautira, E. trib. Vaitepiha R.,/ 17° 46' 30" S. 149° 10' 20" W./ alt. 50m, 19-vii-80, D.A. Craig" (3, CNCI; 1 MNHP). Larvae: penultimate; label data:- "Tiarei, immediately west of Trou du Souffleur, 17° 31' 30" S. 149° 23' 32" W. alt. 10m, 17-ii-87,/ D.A.C." (3, BMNH; 3, BPBM; 3, CNCI; 4, MNHP; 3 UASM; 3, USNM).

Specific epithet.— Because of the probable phylogenetic importance of this species, it is named in honour of the Institut Territorial de Recherches Medicales "Louis Malardé", Papeete, Tahiti. The personnel of this institute and that of ORSTOM, Papeete, provided assistance without which this study would not have been completed.

Diagnosis.—

Pupa: dorsal gill filaments long; thoracic tubercles absent. Larva: hypostoma with three sublateral teeth per side only.

Description.—

Adult Female. Unknown.

Adult Male (single reared specimen). Body: generally blackish-brown; length 0.8 mm. Head: width 0.8 mm, depth 0.6 mm. Eyes: upper ommatidia 0.03 mm in diameter, 18 and 22 respectively across and up eye; lower ommatidia, 0.01 mm in diameter. Clypeus: 0.20 as wide as head. Antenna: length 0.7 mm. Mouthparts: 0.25 length of head depth; mandibles slender, with apical hairs only; lacinia short with small retrorse teeth; palpus 0.7 mm long, distal article 0.3 mm, sensory vesicle spherical, occupying only 0.50 of width of third palpal article, opening less than 0.33 width of vesicle, *ca.* 10 sensillar sockets visible. Thorax: length 0.7 mm; scutum evenly jet black; postpronotal lobe lighter, vestiture of even silver-golden scales; scutellum broadly cone-shaped with obtuse angle, vestiture of long pale hairs crossing at midline; postscutellum light brown; pleuron brown; anepisternal membrane pale. Wing: length 1.7 mm, maximum width 0.6 mm; stem vein hair tuft small, but distinct; basicostal vein with distinct black hairs. Halter: white. Legs: generally brown; pretarsal claw smooth, basal tooth clear, 0.33 as long as claw, *ca.* 24 grappling hooks on each claw. Abdomen: generally dark brown; basal fringe of brown hairs extended to abdominal segment III; tergite II pale medially, light brown laterally, other tergites evenly brown. Genitalia (Fig. 14): gonocoxa 2.0 times as long as basal width; gonostylus *ca.* 2.5 times as long as basal width, terminal spine prominent; ventral plate heart-shaped, bare, anterior arms robust and heavily pigmented, medial notch shallow.

Pupa. (From above male, and one fully developed pharate pupa.). Length: 2.0 mm. Gill: 1.4 mm in length; branching pattern typical; eight slender filaments, subequal in length. Thorax: tubercles absent; cuticle straw coloured and shiny. Abdomen: tergite I bare, with lateral pigment patches; tergite II with small hooks; tergites III and IV with substantial hooks; tergite V bare; tergites VI–VIII with small hooks in single row; sternite III bare; sternites IV–VII with four equally

spaced hooks; caudal spines very short.

Larva. Last instar with dark pupal gills; length 5.7 mm. Body: light brownish-grey with creamy intersegmental regions. Head capsule (Fig. 31): broadest at stemmata, narrowing posteriorly, but not conspicuously so; generally pale in colour; frontoclypeal apotome broadest posteriorly; head-spots colour pattern positive, but faint; anteromedian, anterolateral and posteromedian spots fused, posterolateral spot faint; sensilla number normal; cervical sclerites distinct, but partially fused to postocciput. Stemmata: surrounded by clear area, extended posterodorsally to ecdysial suture. Antenna: extended well beyond labral fan stem, total length 0.39 mm, distal article 0.12 mm, annulation between basal and medial articles insubstantial. Labral fans: with 29 rays, *ca.* 0.73 mm in length; six or seven medial rays shorter and less robust; microtrichia of median rays 1.1 times as long as ray width, no microtrichial pattern (Fig. 59). Hypostoma (Fig. 40): heavily pigmented; median tooth slightly shorter than lateral teeth; three sublateral teeth per side; lateral teeth prominent; one to two paralateral teeth; six to seven lateral serrations per side; hypostomal sensilla, five per side in row. Postgenal cleft: squarish, 1.3 times as wide as deep, rough anteriorly. Postgenal bridge: 1.3 times as long as cleft (Fig. 31). Mandible: apex (Fig. 51) with 10–11 spinous teeth between apical teeth and mandibular serration; distance between serration and spinous teeth as long as width of serration base; serration higher than width as base, anterior edge twice as long as posterior, concave; basal sensillum 0.50–0.33 length of serration, on distinct base. Maxillary palpus: 2.8 times as long as width at base. Mandibular phragma: extended ventrad to 0.50 depth maxillae base. Abdomen: segments increased gradual in size to segment V, then to maximum size, but not suddenly (Fig. 22); posterodorsal cuticle with evenly spaced spine-like tubercles, trichoid and trifid sensilla, 4.5 μm and 3.1 μm long respectively; terga VI with two anterodorsal tubercles (Fig. 22); smaller tubercles on anterior segments (absent from earlier instars); posteroventral tubercles very small. Anal sclerite: with posteroventral arms 2.0 times longer than dorsolateral arms; lateral accessory sclerite consisting of two groups of semifused sclerites, dorsal group larger, or posteroventral arms extended almost around anal proleg. Circlet of hooks: 60 rows of hooks, 14 hooks per row. Anal papillae simple (Fig. 22).

Bionomics.— All material known is from vegetation in small, densely shaded streams and trickles of water. At the Vaitepiha R. site, particulate material in the water was 0.6 mg/L. Noticeable was that the water was clear even during heavy rain.

Phylogenetic Relationships.— *Simulium malardei* is the only Tahitian simuliid possessing six sublateral hypostomal teeth in the larva. This plesiomorphic character state resembles that of the Marquesas Island simuliids (Séchan *in* Klein *et al.*, 1983). Tubercles on the posterodorsal abdomen of the larvae is a character state shared with larvae of the Rarotongan *S. teruamanga* (Craig and Craig, 1986).

Material Examined.— In addition to types I have seen the following:

Tiareí, immediately west Trou du Souffleur, 17° 31' 30" S. 149° 23' 32" W. alt. 10m., 17-ii-87, D.A. Craig (6 early instar larvae, DAC).

<center>*opunohuense* - group</center>

Diagnosis.—

Pupa: thoracic tubercles absent; gill with dorsal filaments shorter than others.

Larva: generally pale; hypostomal median tooth prominent, others not; postgenal cleft squarish; anal papillae simple.

Included taxa.— *Simulium lotii* n. sp. TAHITI; *Simulium opunohuense* n. sp. MOOREA.

<center>*Simulium (Inseliellum) lotii* n. sp.
(Figs. 6, 13, 30, 39, 50)</center>

Simulium sp. ? *cheesmanae* Edwards. Grenier and Rageau, 1960: 733; Grenier and Rageau, 1961b: 174.
Simulium sp. Craig, 1975a: 470.
Simulium sp. "light". Craig, 1983: 534. Schröder, 1985: 5.

Types.— A larva has been chosen as the holotype because definitive association of stages was difficult. The holotype comes from Bain Loti, where morphologically identical specimens are karyologically distinct from sympatric species (Rothfels *in* Craig, 1983).

Holotype. Larva: last instar; slide mount; label data:- "Holotype", "Simulium (I.)/ lotii Craig/ Tahiti, Papeete, Fautaua R., Bain Loti,/ 17° 33' 15" S. 149° 33' 00" W./ 11-vii-80,

D.A. & R.E.G. Craig." (MNHP).

Paratypes. The reared adults chosen as paratypes have associated pupal exuviae closely matching pharate pupal material taken from last instar larvae. However, there is a possibility that some of these specimens could be of *S. exasperans.*

Female: pinned; reared; with pupal exuviae and cocoon as subsidiary material; head and genitalia in vial; label data:- "Paratype", "Simulium (I.)/ lotii Craig/det./ D.A. Craig 1986", "Tahiti, Papeete, Fautaua R.,/ Bain Loti/ 17° 33' 15" S. 149° 33' 00" W. / 08-vii-80,/ D.A. & R.E.G. Craig. Stat. #2" (MNHP). Female: pinned; reared; with pupal exuviae and cocoon as subsidiary material; genitalia in vial; label data:- "Paratype", "Simulium (I.)/ lotii Craig/det./ D.A. Craig 1986", "Tahiti, Tiarei, Fareteuira R./ Cascades de Faarumai,/ 17° 32' 10" S. 149° 23' 48" W./ 21-vii-80,/ D.A. & R.E.G. Craig. Stat. #15" (BMNH). Male: pinned; reared; with pupal exuviae and cocoon as subsidiary material; label data:- "Paratype", "Simulium (I.)/ lotii Craig/ det./ D.A. Craig 1986", "Tahiti, Mataiea, Vaihiria R./ 17° 41' 31" S. 149° 25' 02" W./ alt. 250m. 17-vii-80,/ D.A. & R.E.G. Craig. Stat. #11" (MNHP).

Alcohol material: karyotyped larval remains; label data:- "Paratype", "Simulium (I.)/ lotii Craig/ det./ D.A. Craig 1986", "Tahiti, Papeete, Fautaua R./ Bain Loti,/ 17° 33' 15" S. 149° 33' 00" W./ 8-vii-80,/ D.A. & R.E.G. Craig. Stat. #2" (4, MNHP). Karyotyped larval remains; label data:- as above, but date "11-vii-80/ Stat. #5" (3, BMNH; 4, CNCI). Larvae: label data:- "Paratype", "Simulium (I.)/ lotii Craig/ det./ D.A. Craig 1986", "Tahiti, Paea, Aoua St., 20-vi-73, D.A. Craig." (5, CNCI). Pupa & larvae: label data:- "Paratype", "Simulium (I.)/ lotii Craig/ det./ D.A. Craig 1986", "Tahiti, Papeete, Fautaua R., Bain Loti, 17° 33' 15" S. 149° 33' 00" W. alt. 92m. 15-vii-74, D.A. & R.E.G. Craig" (1 pupa, 3 larvae, DSIR). Larvae: label data:- "Paratype", "Simulium (I.)/ lotii Craig/ det./ D.A. Craig 1986", "Tahiti, Papeete, Fautaua R., Bain Loti, 14-iv-61, J.N. Belkin" (6, USNM). Larva: label data:- "Paratype", "Simulium (I.)/ lotii Craig/ det./ D.A. Craig 1986", "Tahiti, Haapape, Tuauru R.,/ 17° 32' 10" S. 149° 29' 15" W. alt. 60m. 09-vii-80/ D.A. & R.E.G. Craig. Stat. #3." (1,UASM).

Specific epithet.— In reference to "Bain Loti", a pool in the Fautaua River, where this species was first collected. This pool is well known in Tahiti because of the famous French writer and traveller, Pierre Loti. In "Marriage of Loti" (Loti, 1887), "Loti" spent many hours dallying in a pool (now Bain Loti) of the Fautaua River with his beautiful young bride Rarahu.

Diagnosis.—

Larvae: small; pale; head spot pattern positive, spots lightly fused.

Description.—

Adult Female. Body: generally black; length 1.6 mm. Head: black; width 0.6 mm, depth 0.4 mm. Eyes: dark grey; interocular distance 0.50 width of clypeus; frontal angle, 88 degrees; ommatidia 0.013 mm in diameter, *ca.* 27 and 37 respectively across and up eye in middle row. Vertex and frons: subshiny, black, slightly pilose. Clypeus: 0.25 head width; concolourous to slightly lighter than frons, slightly pilose with vestiture of sparse hairs. Antenna: length 0.4 mm; scape, pedicel and basal portion of first flagellomere lighter in colour than remainder. Mouthparts: length 0.50 head depth; mandibles shorter than labrum, with *ca.* 20 very fine teeth; lacinia with *ca.* 16 retrorse teeth; palpus 0.4 mm long, distal article 0.08 mm long, proximal article concolourous with clypeus, sensory vesicle occupying 0.50 width of third article, opening 0.50 width of vesicle, *ca.* 15 sensillar sockets visible. Cibarial pump: space between proximal arms U-shaped, as wide as deep, smooth. Thorax: length 0.3 mm; postpronotum brown, junction with scutum distinct; scutum uniformly black-brown, subshiny with vestiture of very sparse silver scales; scutellum pale yellow, vestiture of very sparse hairs, posterolateral edges slightly concave; postscutellum, concolourous with scutellum. Wing: length 1.7 mm, maximum width 0.7 mm; stem vein hair tuft not prominent. Halter: pale yellow. Legs: forelegs paler than others; pretarsal claw with basal tooth 0.50 length of claw. Abdomen: generally dark brownish-grey; basal fringe of insubstantial golden hairs extended back to abdominal segment II; tergites increasing in size posteriorly, subshiny; tergites VII and VIII with long dark hairs. Genitalia (Fig. 6): cercus, bluntly cone-shaped in ventral view; hypogynial valves divergent smoothly posteriorly, almost in contact distally, smoothly rounded apically; stem of genital fork long and thin, lateral sclerites triangular with acute anterior apex; sternite VIII medial pigmented area subrectangular. Spermatheca: slightly ovoid; no pattern; not strongly

pigmented; unpigmented area at junction of sperm duct normal.

Adult Male. Body: generally black; length 2.3 mm. Head: width 0.7 mm, depth 0.6 mm. Eyes: upper ommatidia 0.05 mm in diameter, 18 and 20 per row respectively, up and across eye; lower ommatidia 0.03 mm in diameter, 34 and 28 per row respectively, up and across eye. Clypeus: black; 0.25 as wide as head; vestiture of long black hairs. Antenna: uniformly dark grey; length 0.45 mm. Mouthparts: 0.66 length of head depth; labrium pale laterally; mandibles with *ca.* 20 fine teeth; lacinia with *ca.* 15 retrorse teeth; palpus, uniformly blackish-brown, 0.38 mm long, sensory vesicle occupying 0.50 width of third palpal article, opening less than 0.50 width of vesicle, *ca.* 15 sensillar sockets visible. Thorax: length 0.3 mm; scutum and postpronotum uniformly matt black, anterior vestiture of long golden scales; scutellum lighter than scutum, vestiture of dense black hairs; postscutellum black; pleuron dark brown. Wing: length 1.6 mm, maximum width 0.8 mm. Halter: dark grey. Legs: dark; pretarsal claw smoothly curved and slender, *ca.* 19 grappling hooks on each claw. Abdomen: black; basal fringe of long black hairs, extended to abdominal segment IV; tergites V–VI with pale areas laterally; sternites with yellowish-brown mottled area. Genitalia (Fig. 13): gonocoxa 2.3 times as long as basal width; gonostylus *ca.* 0.50 as wide as long, curved with one blunt terminal spine; ventral plate extensively haired, broadly rounded posteriorly, posterolateral edges concave, distinct lateral angle, anterior arms heavily pigmented, anteromedial area domed with deep medial incision.

Pupa. Length: 2.4 mm. Gill: length 1.6 mm; branching pattern normal, dorsal pair of filaments 0.50 length of contiguous pair; markedly varied, both same length, or one, or other shorter, length from 0.25–0.66 length of other contiguous pair, a few with one filament on that branch (*i.e.,* seven filaments in total). Thorax: tubercles absent; cuticle light brown, shiny. Abdomen: tergite I bare; tergite II with small hooks and trichoid sensilla; tergites III–IV with substantial hooks; tergite V bare; tergites VI–VIII with small hooks; tergite IX with field of small spines; sternites IV and V with two pairs of hooks; sternites VI and VII with hooks evenly spaced; caudal spines, small to absent.

Larva. Length: last instar with dark pharate pupal gills, 4.3–4.9 mm. Body: greyish-brown with pale intersegmental regions as broad as colour bands. Head capsule (Fig. 30): essentially parallel-sided; generally pale to light brown, variable; frontoclypeal apotome broadest at posterior, pale anteriorly, light brown posteriorly; spot pattern positive with anteromedian, anterolateral and posterolateral spots lightly fused; cervical sclerites distinct; sensilla, normal number. Antenna: longer than labral fan stem, distal article 0.1 mm, proximal articles 0.47 mm; basal article light brown. Labral fans: with 31–33 rays, *ca.* 1.1 mm in length, the six medial rays less substantial; microtrichia of medial rays 2.2 times longer than ray width; microtrichial pattern only on medial rays, with 6–7 small microtrichia interspersed with larger microtrichia. Hypostoma (Fig. 39): median tooth prominent; other teeth subequal in length, tips in straight line, four sublateral teeth per side, two paralateral teeth, three or four small lateral serrations and four to six hypostomal sensilla per side; lateral and paralateral teeth with tines. Postgenal cleft: squarish. Postgenal bridge: three times longer than cleft. Mandible: apex (Fig. 50) with nine to 10 spinous teeth; area between teeth and serrations as wide as serration base; serration as high as basal width, anterior edge 1.5 times longer than posterior edge, edges straight; sensillum small, not on serration. Maxillary palpus: 2.0 times as long as width at base. Mandibular phragma: extended ventrad to 0.50 depth of maxilla base. Abdomen: segments I–V increased slightly in size to VI, segment VII markedly larger, segment VIII largest; posteroventral tubercles almost absent; posterodorsal cuticle with low ovoid tubercles, and trichoid sensilla, 22.5 μm long. Anal sclerite: posteroventral arms 2.0 times longer than dorsolateral arms; lateral accessory sclerite fused to posteroventral arm via narrow junction. Circlet of hooks: 92 rows of hooks, 15–16 hooks per row. Anal papillae: simple.

Bionomics.— *Simulium lotii* is widespread on Tahiti and occurs with *S. tahitiense, S. exasperans* and *S. oviceps* in shaded, larger rivers and streams. There is a tendency for the larvae to be on vegetation (Schröder, 1985).

Phylogenetic Relationships.— This species was first recognised by Grenier and Rageau (1960) as *Simulium* sp. (= ? *cheesmanae*). Examination of their material (Craig, 1983), showed that it was conspecific with material described as *Simulium* sp. (Craig, 1975a) and material termed "light" by Craig (1983). The pupae, and female genitalia of material described here agree with the material described by Grenier and Rageau (1960) and which I have examined. However, the ventral plate of the male described here is more cone-shaped apically than that of the male described by Grenier and Rageau (*loc. cit.*). This leaves open the possibility of a misassociation either by Grenier and Rageau, or me, or, the presence of another species similar to *S. lotii*.

Material Examined.— In addition to the types, I have seen the following:

Papeete, Faataua (sic) R., Bain Loti, 17° 33' 15" S. 149° 33' 00" W. 00-ix-1954, 00-vi-1959, Grenier, P. and J. Rageau (slide material of pharate male, IP). 11-vii-74, D.A. & R.E.G. Craig (larvae in alcohol, BMNH; BPBM; CNCI; DSIR).
Pirae, Pirae R., undated material, Grenier, P. and J. Rageau. (slide material of pharate female, IP).
Tiarei, Fareteuira R., Cascades de Faarumai, 17° 32' 10" S. 149° 23' 48" W. 21-vii-80, D.A. & R.E.G. Craig (1 ♀, 1 ♂, DSIR).
Mataiea, Vaihiria R., 17° 41' 31" S. 149° 25' 02" W. alt. 250 m. 17-vii-80, D.A. & R.E.G. Craig (1 ♀, 1 ♂, BMNH; 1 ♂,

CNCI).

Simulium (Inseliellum) opunohuense n. sp.
(Figs. 7, 33, 42, 54)

Types.—

Holotype. Larva: last instar; as slide mount; label data:- "Holotype", "Simulium (I.) opunohuense Craig/ det./ Craig 1986", "Polynesia, Moorea, /Opunohu V. Marae de Titiroa, 17° 32' 00" S. 149° 49' 40" W./26-ii-84, P. Schröder" (MNHP).

Paratypes. Larvae: Penultimate instars; as slide mounts; other earlier instars in alcohol; label data:- "Paratype", "Simulium (I.) opunohuense Craig/ det./ Craig 1986", "Polynesia, Moorea, Opunohu V.,/ nr. road leading to Pao Pao, 17° 31' 42" S. 149° 50' 00" W./26-ii-84, P. Schröder" (1 slide, 5 larvae, BMNH; 1 slide, 5 larvae, MNHP).

Specific epithet.— Named after the Opunohu Valley, Moorea, where the larvae and presumably the adult were found.

Diagnosis.—

Female adult: jet black; sternite VIII without median pigmented region. Larva: head spot pattern positive, spots separate; accessory sclerite of anal sclerite absent.

Description.—

Adult Female (single specimen, see Phylogenetic Relationships). Body: evenly jet black; length 2.5 mm. Head: width 0.6 mm, depth 0.5 mm. Eyes: interocular distance 0.33 width of clypeus; frontal angle 45 degrees; ommatidia 0.02 mm in diameter, *ca.* 26 and 36 respectively across and up eye in middle row. Clypeus: as wide as long, 0.20 as wide as head, densely pilose, vestiture of sparse golden hairs. Antenna: length 0.4 mm; scape and pedicel dark orangey-brown; flagellomeres dark. Mouthparts: length 0.33 head depth; mandibles as long as labrum, with *ca.* 14–16 small sharp teeth; lacinia as long as labrum, with *ca.* 24 very sharp retrorse teeth; palpus, 0.6 mm long, distal article 0.2 mm long, sensory vesicle elongate, occupying 0.50 length and 0.50 width of third article, opening 0.50 width of vesicle, *ca.* 50+ sensilla sockets visible. Cibarial pump: space between proximal arms U-shaped, 1.5 times wider than deep, smooth. Thorax: length 0.9 mm; postpronotal lobe slightly pilose; scutum evenly jet black, vestiture of sparse golden hairs, denser posteriorly; scutellum and post scutellum concolourous with scutum; scutellum with slightly concave sides, vestiture of long black hairs; postscutellum slightly pilose. Wing: length 2.0 mm, maximum width 0.9 mm; stem vein hair tuft insubstantial. Halter: dark yellow. Legs: dark with dense vestiture of fine yellow hairs; pretarsal claw very slender, basal tooth longer than 0.50 length of claw. Abdomen: evenly black; basal fringe of golden hairs extended back to abdominal segment II. Genitalia (Fig.7): cercus in ventral view bluntly rounded; hypogynial valves diverging slightly then converging posteriorly, extended 0.50 way along anal lobe; stem of genital fork smooth thin, with angulate anterior apex, dark brown with pigment continuing posteriorly into fork; lateral sclerites sharply triangular, anterior apex forming acute angle; sternite VIII pigmented evenly over full width, slightly darker medially. Spermatheca: ovoid; slight reticulate pattern; not heavily pigmented; clear area at junction of sperm duct substantial .

Adult Male.- Unknown.

Pupa. (based on pharate pupal material from holotype larva). Gill: length 2.1 mm; eight filaments; branching pattern typical, two dorsal-most filaments equal in length, 0.50 length of other filaments. (Possibly variable; one filament shorter and one almost absent). Thorax: tubercles probably absent.

Larva. Last instar larva with dark pharate pupal gills; length 2.8–3.4 mm. Body: pale grey with narrow intersegmental regions. Head capsule (Fig. 33): generally pale to light brown; frontoclypeal apotome pale anteriorly, light brown posterolaterally; spot pattern positive, anteromedian and posteromedian spots fused, occasionally central spots surrounded by very light brown; cervical sclerites small, but distinct. Stemmata: with posterior light brown area. Head cuticle: essentially smooth, corrugated laterally; sensilla number normal. Antenna: longer than labral fan stem; distal, proximal articles and antennal base light brown. Labral fans: with 29 substantial and three insubstantial rays, *ca.* 0.73 mm. in length, darker than head; microtrichia of medial rays up to 2.0 times longer than ray width, pattern of seven or eight small microtrichia between larger ones. Hypostoma, postgenal cleft and bridge (Fig. 33, 42): essentially as for *S. tahitiense*; five hypostomal sensilla per side. Mandible: apex (Fig. 54) with eight spinous teeth; distance between spinous teeth and mandibular serration smaller than serration base width; serration as high as basal width, sharply pointed and with concave sides; lengths of anterior and posterior sides equal; sensillum peg-like. Maxillary palpus: 3.0 times as long as width at base. Mandibular phragma: extended ventrad to 0.33 depth of maxilla base. Abdomen: segments I–IV increased smoothly laterally to maximum size at segments V and VI; posteroventral tubercles very small; posterodorsal cuticle with ovoid scales with longitudinal striae, and with trichoid sensillae 6.9 μm long. Anal sclerite: posteroventral arms 1.5 times longer than dorsolateral arms; accessory sclerite absent. Circlet of hooks: 81 rows of hooks, 14–16 hooks per row. Anal papillae:

simple.

Bionomics.— The holotype larva was collected from a small, heavily shaded rocky stream, the bottom of which was covered with red epilithic algae. The paratype larvae came from further downstream and were on trailing roots of trees. The water was 5 cm deep with velocity *ca.* 50 cm/s (P. Schröder, pers. comm., 1987).

Phylogenetic Relationships.— Larvae of *S. opunohuense* are morphologically very similar to those of *S. lotii*, differing mainly in the more distinct head spot pattern. However, the female adults of the two species differ in a number of characteristics, such as colour of body and legs, and shape and sclerotization of parts of the genitalia. Cytological examination will no doubt show these two taxa to be very closely related. The single adult collected by Puleston, while probably of *S. opunohuense*, was not included in the types series because the association to the immature stages was not definitive. The possibility remains that if this unique female has not been correctly associated, *S. opunohuense* may be conspecific with *S. lotii* and the adult is then that of an undescribed species.

Material Examined.— In addition to types I have seen the following:

FR. POLYNESIA, Opunohu Bay (word "Bay" crossed out), vii.6.1959, D.E. Puleston (♀ pinned; head and genitalia cleared and in vial, USNM).

tahitiense - group

Diagnosis.—

Pupa: scutellum bluntly pointed dorsally. Larva: body expanded rapidly ventrally at segment VI, decreased abruptly at segment VIII (Fig. 23); head spot pattern positive; margins of head capsule not markedly convex (Fig. 35).

Included taxa.— *S. tahitiense* Edwards, *S. exasperans* n. sp. and *Simulium* "IIS"; TAHITI.

Simulium (Inseliellum) exasperans n. sp.
(Figs. 5, 12, 19, 49)

Types.—

Holotype. Female: pinned; reared; with pupal exuviae and cocoon as subsidiary material; label data:- "Holotype", "Simulium (I.)/ exasperans Craig", "Tahiti, Punaauia, Punaruu R., / 17° 38' 20" S. 149° 35' 05" W. /alt. 120m. 07-vii-80, / D.A. Craig. Stat. #1" (MNHP).

Paratypes. Adults: pinned; reared; with exuviae and cocoons as subsidiary material; label data as for holotype (2 ♂, BMNH; 1 ♂, BPBM; 1 ♀, 2 ♂, MNHP). Male: pinned; reared; with exuviae and cocoon as subsidiary material; label data:- "Paratype", "Simulium (I.)/ exasperans Craig", "Tahiti, Papeete, Fautaua R., Bain Loti, /08-vii-80, 17° 33' 15" S. 149° 33' 00" W./ D.A.Craig. Stat. #2" (1 ♂, MNHP). Females: pinned; reared; with exuviae and cocoons as subsidiary material; label data as for Bain Loti, but date as "11-vii-80.Stat. #5" (1 ♀ each, BMNH; BPBM; CNCI; MNHP). Male: slide mount; label data as for Bain Loti, but date:- "08-vii-1974" (DAC). Female: pinned; reared; with exuviae and cocoon as subsidiary material; label data:- "Tahiti, Tiarei, Fareteuira R., Cascades de Faarumai,/17° 32' 10" S. 149° 23' 48" W./ 21-vii-80, / D.A. & R.E.G. Craig. Stat. #15" (1 ♀, BMNH). Male and female: pinned; reared; with exuviae and cocoons as subsidiary material; label data:- "Tahiti-iti, Tautira, Vaitepiha R.,/17° 46' 30" S. 149° 10' 21" W./ alt. 50m. 19-vii-80,/ D.A. & R.E.G. Craig. Stat. #13" (1 ♀, 1 ♂, MNHP). Males and females: pinned; reared; with exuviae and

cocoons as subsidiary material; label data:- "Tahiti, Mataiea, Vaihiria R.,/ 17° 41' 31" S. 149° 25' 02" W./ alt. 250 m. 17-vii-80, /D.A. & R.E.G. Craig. Stat. #11" (2 ♀, 1 ♂, each BMNH; BPBM; CNCI; MNHP; 1 ♀, DSIR). Female: pinned; reared; with exuviae and cocoon as subsidiary material; label data:- "Tahiti, Mataiea, E. Lac Vaihiria, /17° 40' 58" S. 149° 24' 51" W./ alt. 430m. 22-vii-80, /D.A. & R.E.G. Craig. Stat. #16" (1 ♀, MNHP). The following material was previously identified as *S. tahitiense.* Female: pinned; reared; with exuviae and cocoon as subsidiary material; label data:- "Tahiti, Baini (sic) /Loti /April 14, 1961. /J.N. Belkin #35" (1 ♀, USNM). Female: pinned; reared; with exuviae and cocoon as subsidiary material; label data:- "Tahiti, Paea, / March 30 1961, /D.G. Basio #26" (1 ♀, USNM). Female: pinned; reared; with exuviae and cocoon as subsidiary material; label data:- "Tahiti, Paea,/ April 2 1961, /J.N. Belkin #28" (1 ♀, USNM). Pupa: with larval exuviae; label data:- "Tahiti, Punaruu R., / 1969. B. Hocking" (MNHP). Larva: last instar; label data:- "Tahiti, Mataiea, Vaihiria R., / 17° 41' 31" S. 149° 25' 02" W./ alt. 250m. 17-vii-80,/D.A. & R.E.G. Craig" (BMNH). Pupal and larval material: as slide mounts; two last instar larvae; label data:- "Tahiti. Paea, Aoua St., /20-vi-73, D.A. Craig" (BMNH; MNHP). Alcohol material: Pharate adult; label data:- "Papeete, Fautaua R., Bain Loti,/ 17° 33' 15" S. 149° 33' 00" W./ 08-vii-80, D.A. & R.E.G. Craig. Stat. #2" (CNCI). Larvae: label data:- "Tahiti, Paea, Aoua Str., /20-vi-73, D.A. Craig" (larvae, 2 pupae each BMNH; BPBM; MNHP; larvae, CNCI; DSIR; USNM). Larvae: label data:- "Tahiti, Paea,/ 'Robinson's Place', /28-iii-61. J. N. Belkin" (5, USNM). Larvae and pupa: label data:- "Paea, Public Garden, / 03-vii-81, D.A. Craig" (6 larvae, BMNH; 5 larvae, 1 pupa, MNHP).

Specific epithet.— Based on the Latin word "exaspero", meaning "to irritate", in reference to the difficulty of associating the stages of this species.

Diagnosis.—

Pupa: thoracic tubercles absent; dorsal gill filaments long.

Larva: *tahitiense*-like, but anal papillae simple.

Recognition.— This species is very difficult to distinguish in all stages from both, *S. tahitiense* and *S. lotii.* Consequently, further work is needed to clarify the limits of the taxa. Adults of *S. tahitiense*, without the associated pupal exuviae, are virtually impossible to separate from *S. exasperans.* For this reason alone, reared adults are absolutely necessary for taxonomic studies on Tahitian simuliids.

Description.—

Adult Female. Body: generally blackish-brown; length 1.5–2.1 mm. Head: very dark brown; width 0.5 mm, depth 0.4 mm. Eyes: dark red; interocular distance 0.50 width of clypeus; frontal angle, 75 degrees; ommatidia 0.02 mm in diameter, *ca.* 24 and 26 respectively across and up eye in middle row. Post-ocular hairs black; extended to eye margin. Clypeus: 0.16 mm, lighter than frons, margins pilose, vestiture of sparse black hairs. Antenna: length 0.4 mm; scape, pedicel and anterior region of first flagellomere yellow, remaining flagellomeres dark brown. Mouthparts: length 0.4 times head depth; mandibles, as long as labrum, with *ca.* 21 teeth; lacinia with *ca.* 16 retrorse teeth; palpus, 0.4 mm long, distal article 0.13 mm long, proximal article concolourous with clypeus, remainder lighter, sensory vesicle occupying 0.50 width of third article, opening 0.50 width of vesicle, eight to 10 sensillar sockets visible. Cibarial pump: space between proximal arms flat, smooth, three times as wide as deep. Thorax: length 0.8–0.9 mm; scutum evenly very dark brown; postpronotal lobes with posterior margins lighter, sparse, even vestiture of silver-golden scales; scutellum cone-shaped, forming slightly obtuse angle, lateral margins straight, vestiture of sparse, long golden and black hairs; postscutellum, concolourous with scutum, pilose in some views; pleuron evenly dark brown. Wing: length 1.9–2.1 mm, maximum width 0.8–0.9 mm; stem vein hair tuft substantial; basicostal vein with dense black hairs. Halter: pale. Legs: as for *S. tahitiense.* Abdomen: evenly very dark brown; basal fringe of golden hairs extended back to posterior of abdominal segment II. Abdomen: tergites II–VII mottled with lighter markings; vestiture of very sparse golden scales, black on tergites VIII and IX; pleural and sternal regions pilose and greyish. Genitalia (Fig. 5): cercus pointed distally in ventral view; anal lobe curving smoothly medially; hypogynial valves diverging distally, but converging apically, very blunt, extended just to anal lobes; stem of genital fork thin, smooth, lateral sclerite with rounded angulate anterior apex and long thin posterior arm; sternite VIII with pigmented median region narrow posteriorly, expanded anteriorly. Spermatheca: ovoid; no pattern; not heavily pigmented;

clear area at junction of sperm duct normal.

Adult Male. Body: generally blackish-brown; length 1.6–1.7 mm. Head: width 0.6 mm, depth 0.5 mm. Eyes: upper ommatidia 0.09 mm in diameter, 16 and 18 per row respectively across and up the eye; lower ommatidia, 0.03 mm in diameter. Clypeus: 0.20 as wide as head; vestiture of sparse black hairs. Antenna: length 0.4 mm; evenly dark brown. Mouthparts: 0.33 length of head depth; mandibles very thin, no teeth, only fine apical hairs; lacinia with *ca.* 23 small retrorse teeth; palpus 0.4 mm long, distal article 0.2 mm, sensory vesicle spherical, occupying 0.66 of width of third palpal article, opening less than 0.50 width of vesicle, *ca.* 10 sensillar sockets visible. Thorax: length 0.6 mm; scutum evenly black; postpronotal lobes slightly lighter; scutellum lighter, pale posteriorly, vestiture of long black hairs crossing in midline; postscutellum dark brown, slightly pilose; pleuron brown. Wing: length 1.5–1.7 mm, maximum width 0.7–0.8 mm; stem vein hair tuft small, but distinct. Halter: brown. Legs: as for *S. tahitiense.* Abdomen: generally blackish- brown; basal fringe of black hairs extended to abdominal segment II; tergite II pale; III–VII mottled brown; VIII–X dark brown; tergites III, VI, VII in some views pilose laterally. Genitalia (Fig. 12): gonocoxa 2.0 times as long as basal width; gonostylus approximately 3.5 times longer than basal width, curved with one blunt terminal spine; ventral plate with broadly rounded apex, concave posterolaterally, anterior arms angulate and strongly pigmented, anteromedial notch barely present; hairy region narrow in middle.

Pupa. Length 2.0–2.5 mm. Gill (Fig. 19): length 0.9–1.0 mm; branching as for *S. tahitiense.* Head and thoracic cuticle: without tubercles; cuticle straw coloured and shiny. Abdomen: tergites essentially as for *S. tahitiense;* tergite I without tubercles, but with small scales; tergite II without hooks, but with anteriorly directed short hairs; tergites III and IV hooks slender; those of tergites VI–IX small and in single rows; caudal spines essentially absent; sternites as for *S. tahitiense.*

Larva. Virtually indistinguishable from *S. tahitiense.* Head capsule: paler than *S. tahitiense;* to very pale (similar to *S. lotii*). Labral fans: with 29 rays (15s ray robust others finer), *ca.* 0.45 mm. in length; microtrichia of medial rays up to 1.6 times longer than ray width; no microtrichial pattern. Hypostoma: as for *S. tahitiense* (Fig. 44). Abdomen: posterior shape not as pronounced as for *S. tahitiense;* ventral tubercles not prominent; posterodorsal cuticle with laterally elongated and sharply pointed sculpting; trichoid sensilla 16.0 μm. Anal sclerite: with posteroventral arms 2.0 times longer than dorsolateral arms. Circlet of hooks: as for *S. tahitiense.* Anal papillae: simple.

Bionomics.— Larvae tend to be found on vegetation in well shaded, larger streams. In some situations it forms almost the complete population, *e.g.,* Aoua Stream, Paea, otherwise, it is found with *S. lotii, S. oviceps* and *S. tahitiense.*

Phylogenetic Relationships.— It is interesting that no karyological evidence of *S. exasperans* was detected by Rothfels (*in* Craig, 1983). However, this species may be cytospecies "IIS" which Rothfels (*loc. cit.*) found only on Tahiti-iti, but *S. exasperans* is also found extensively on Tahiti-nui. Association of stages of this species was particularly difficult. The connection between larval and pupal stages was eventually made via some pupae retaining their larval exuviae in the cocoon, and by partially ecdysed pharate adults.

Material Examined.— In addition to types, I have seen the following:

Alcohol material.
Papeete, Fautaua R., Bain Loti, 17° 33' 15" S. 149° 33' 00" W. 15-vii-74, (1 pupa, CNCI); 1-vii-81, (10 pupae, BMNH), D.A. & R.E.G. Craig.
Papenoo, Papenoo V., 22-x-28. 17° 36' 22" S. 149° 25' 08" W. A.M. Adamson (2 pupae, BPBM).
Tiarei, Onofea R., 17° 33' 30" S. 149° 23' 47" W. alt. 110m. 14-vii-80, D.A. & R.E.G. Craig (3 pupae, UASM)
Mataiea, Vaihiria R., 17° 41' 31" S. 149° 25' 02" W. alt. 250m. 17-vii-80, D.A. & R.E.G. Craig (4 pupae, BPBM).
Tautira, (Tahiti-iti), E. trib. Vaitepiha R., 17° 46' 30" S. 149° 15' 20" W. alt. 50m. 14-vii-80 (3 pupae, DSIR), 19-vii-80 (3 pupae, USNM), D.A. & R.E.G. Craig; E. trib. Vaitepiha R., 17° 46' 58" S. 149° 10' 39" W. alt. 50m. 02-vii-81. D.A. Craig (5 larvae, BPBM).
Teahupoo, (Tahiti-iti), Tiirahi R., 17° 51' 05" S. 149° 14' 15" W. 20-vii-80, D.A. & R.E.G. Craig (4 pupae, UASM).
Tauemaui, (Tahiti-iti), Fanaa R., 15-ii-84, P. Schröder (1 pupa, MNHP).
Paea, Public Gardens, 03-vii-81, D.A. Craig (larvae, DAC).
Punaauia, Punaruu R., 17° 38' 20" S. 149° 35' 05" W. alt. 120m. 27-iv-69, B.M. Hocking (1 pupa, UASM); 7-vi-80, D.A. & R.E.G. Craig (2 pupae, UASM); 17-vii-80, P. Schröder (5 pupae, MNHP).

Simulium (Inseliellum) tahitiense Edwards
(Figs. 9, 16, 21, 23, 35, 44, 56, 65, 71-73)

Simulium tahitiense Edwards, 1927: 242. Lectotype female (by present designation), TAHITI. Edwards, 1935: 35. Smart, 1945: 242. Grenier and Rageau, 1960: 728. Grenier and Rageau, 1961b: 174. Rubtsov, 1974: 242, 244. Craig, 1975a: 468. Crosskey, 1981: 8. Craig, 1983: 534. Schröder, 1985: 17.

Simulium (Inseliellum) tahitiense Edwards. Crosskey, 1987: 388.

Types.—

Lectotype. Female: pinned; label data:- "Lectotype", "Syntype", "Tahiti. Tautira /9.viii.25 /Miss Cheesman B.M. 1925. 392", "Simulium tahitiense Edw", "Simulium tahitiense Edw /Syntype ♀,/det. R.W. Crosskey, 1979", "Simulium (I) tahitiense Edw. /det./ D.A. Craig 1986" (BMNH).

Paralectotype. Female: pinned; label data:- as for lectotype (BMNH).

Diagnosis.—

Pupa: gill filaments long; thoracic tubercles rounded.

Larva: head spots positive; general body colour dark; anal papillae complex.

Recognition.— Larvae of this species are morphologically varied, particularly so in size, colour and shape of body. Some of the apparent variation may be due to the difficulty of, as yet, clearly separating the similar stages of *S. exasperans*.

Description.—

Adult Female. Body: generally dark brown; length 1.5–1.9 mm. Head: dark brown, slightly pollinose; width 0.71 mm, depth 0.55 mm. Eyes: interocular distance 0.50 width of clypeus; frontal angle, 90 degrees; ommatidia 0.012 mm in diameter, *ca.* 31 and 43 respectively, across and up eye in middle row. Vertex: dark brown. Frons and clypeus pilose; latter with sparse golden hairs. Clypeus: as long as wide; apex with small medial projection. Antenna: length 0.47 mm; scape, pedicel and proximal portion of first flagellomere lighter in colour than remainder. Mouthparts: length less than 0.50 head depth; mandibles as long as labrum, with 22 fine teeth; lacinia with *ca.* 21 retrorse teeth; palpus, 0.46 mm long, distal article 0.23 mm long, sensory vesicle spherical, occupying 0.50 width of third article, opening 0.50 width of vesicle, *ca.* 13 sensillar sockets visible. Cibarial pump: space between proximal arms U-shaped, smooth, as wide as deep. Thorax: dark brown, lightly pilose; length 1.1 mm; postpronotal lobe pollinose at junction with scutum (in dorsal view); scutum uniformly dark brown, vestiture of fine silver scales; scutellum pale brown, angle of posterior apex obtuse, sides slightly concave, vestiture of sparse black hairs; postnotum dark brown; pleuron medium brown. Wing: length 1.8–2.5 mm, maximum width 0.8–1.2 mm; stem vein hair tuft distinct; hairs on basicosta not prominent. Halter: pale gray. Legs: forecoxa concolourous with pleuron; trochanter, femur and most of tibia mottled yellow-brown; distal portion of tibia and tarsus dark brown; mid- and hind leg as for fore leg; hind basitarsus yellow with distal portion and tarsomeres mottled yellow and dark brown; pretarsal claw slender with sharp apex, basal tooth 0.50 length of claw, lying subparallel to claw. Abdomen: generally dark brown; basal fringe of golden hairs extended to segment II; tergites slightly pollinose, mottled, vestiture of dark hairs; posterior tergites subshining with sparse dark hairs; sternum pale gray. Genitalia (Fig. 9): cercus, in ventral view, slightly curved laterally, curved posteromedially; stem of genital fork, thin, smooth, lateral sclerite triangular with anterior apex forming acute angle, directed laterally, notched, or not; hypogynial valves slightly curved medially, broadly rounded posteriorly, extended to anal lobes; sternite VIII with ovoid median pigmented region. Spermatheca: slightly ovoid; not densely pigmented; no reticulation; unpigmented area at junction of sperm duct normal.

Adult Male. Body: generally dark brownish-black; length 1.6–1.9 mm. Head: width 0.5 mm, depth 0.4 mm. Eyes: upper ommatidia, 0.04 mm in diameter, 12 rows both up and across eye; lower ommatidia 0.1 mm in diameter. Clypeus: 0.20 as wide as head. Antenna: total length 0.3 mm. Mouthparts: 0.50 length of head depth; mandibles 0.33 length of labrum; lacinia as long as labrum, no retrorse teeth, apex hairy; palpus 0.4 mm long, distal article 0.2 mm, sensory vesicle spherical, occupying only 0.33 of width of third palpal article, opening 0.50 width of vesicle, *ca.* 10 sensillar sockets visible. Thorax: length 0.7 mm; postpronotal lobe pale; scutum evenly dark brown to black, vestiture of moderately long, golden scales; scutellum pale, slightly convex laterally, forming right angle at apex, vestiture of sparse, long black hairs; postscutellum dark brown; pleuron brown. Wing: length 1.4–1. 6 mm, maximum width 0.6–0.7 mm; stem vein hair tuft small, but prominent. Halter: greyish brown. Legs: coxae brown, trochanter and portions of femur and tibia pale, banding distinct, vestiture of dense black hairs; pretarsal claw with *ca.* 23 grappling hooks on each claw. Abdomen: brown; vestiture of very sparse golden scales; basal fringe of pale hairs extended to abdominal segment II; tergites V–VII mottled. Genitalia (Fig. 16): gonocoxa 1. 8 times as long as basal width; gonostylus approximately 2.5 times as long as basal width, single blunt terminal spine; ventral plate with median posterior apex rounded, slightly convex sides expanded laterally to broadly rounded angle, extended anteriorly to pigmented arms with rounded apices, anteromedially slightly domed, with broad medial notch, median hairy patch, slightly expanded anteriorly.

Pupa. Length: 1.8–2.4 mm male, 1.9–2.3 mm female. Gill (Fig. 21): length 0.8–1.2 mm male, 0.7–1.1 mm female; branching pattern typical, dorsal-most filament long, often reflexed posteriorly over thorax under cocoon. Thorax: cuticle light brown; tubercles rounded (Fig. 71–73); scutellum in lateral view with distinct blunt peak. Abdomen: tergite I bare, tergites II–IV with anteriorly directed hooks, tergite V bare, tergites VI–VIII with fine spine combs; sternites IV and V with hooks close to mid-line, those on sternites VI and VII more lateral, evenly spaced; caudal spines absent; terminal caudal sclerites, distinct, angular.

Larva. Last instar with dark pharate pupal gills; length 3.9–4.9 mm. Body: greyish with anterior intersegmental regions light, producing a banded appearance. Head capsule (Figs. 35, 65): generally dark brown to blackish; frontoclypeal

apotome pale anteriorly, very dark posteromedially; spot pattern generally positive, or posteromedian and posterolateral spot-two, negative, or concolorous with surrounding head cuticle; apotome with anterior pale area extended posteriorly along ecdysial line to posterolateral spot-one; cervical sclerites distinct. Stemmata: surrounded by small clear area, with, or without, curved anterodorsal mark. Head cuticle: corrugated transversely, bent, or not, around anteromedian head spots in form of U- or V- shaped mark anteriorly; sensilla number normal. Antenna: as long as labral fan stem, distal article 0.1 mm, proximal articles 0.2 mm. Labral fans: with 30–33 rays, *ca.* 0.45 mm in length; microtrichia of medial rays up to 1.4 times longer than ray width, no microtrichial pattern. Hypostoma (Fig. 44): median tooth protruded, other teeth in line sloped posterolaterally; five sublateral teeth per side; lateral tooth slightly higher and broader; one paralateral tooth; two to three lateral serrations; six to eight hypostomal sensilla per side. Postgenal cleft: wider than deep, squarish, with either flat or slightly bifurcate apex. Postgenal bridge: 2.3 times length of cleft (Fig. 35). Mandible: apex (Fig. 56) with nine to 11 spinous teeth; distance between spinous teeth and mandibular serration less than 0.50 width of serration base; serration as high as basal width; sensillum small and not on serration. Maxillary palpus: 3.0 times as long as width at base. Mandibular phragma: extended ventrad to 0.33 depth of maxilla base. Abdomen: segments increased gradually in size to segment V; segment VI markedly enlarged ventrally; at segment VIII size reduced sharply (Fig. 23); ventral tubercles placed laterally; posterodorsal cuticle with low, laterally ovoid tubercles and with trichoid sensilla, 9.2 µm long. Anal sclerite: with posteroventral arms 3.0 times longer than dorsolateral arms; lateral accessory sclerite absent, but in darker specimens evident as lightly pigmented disc. Circlet of hooks: 123 rows of hooks, 21–23 hooks per row. Anal papillae: complex (Fig. 23).

Bionomics.— *Simulium tahitiense* is the most wide-spread species in Tahiti. Its larvae are found mainly in the larger rivers, in dense aggregations on and under large boulders in strong flow. If vegetation trails in high velocity water it usually supports large populations of *S. tahitiense* also. In the Papanoo Valley and elsewhere, the adults form dense swarms around humans and cause considerable nuisance although they do not bite. Larvae of the ephydrid *Apulvillus cheesmanae* Edwards (W. N. Mathis, pers. comm., 1983) are found with many of the larger aggregations of *Simulium tahitiense*. Although extremely slow moving there is a possibility that *A. cheesmanae* larvae are predaceous on the simuliid larvae. *S. tahitiense* larvae can be found in almost all the other simuliid habitats in Tahiti. In more shaded localities, such as at Bain Loti, it is associated with *S. lotii* and *S. exasperans* larvae, but its larvae prefer hard substrate to vegetation. Schröder (1985) provides details of the feeding behaviour of larvae of this species.

Material Examined.— In addition to types, I have seen the following:

Papeete, Fautaua R., Bain Loti. Tahiti, Baini (sic) Loti, April 14, 1961, J.N. Belkin #35 (4 ♀, USNM); 17° 33' 15" S. 149° 33' 00" W. alt. 92m, 11-vii-74 (larvae, DSIR; UASM), 15-vii-74 (larvae, UASM), 16-vii-74 (larvae, UASM), 07-vii-80 (larvae, CNCI), 08-vii-80 (1 ♂, CNCI; 2 ♀, DSIR), 11-vii-80 (5 ♀, 5 ♂, BMNH; 5 ♀, 5 ♂, BPBM; 1 ♀, 5 ♂, CNCI; 1 ♀, DSIR; 1 ♂, UASM; 6 ♀, 2 ♂, USNM; karyotyped larvae, BMNH, UASM; larvae, UASM) D.A. & R.E.G. Craig.

Haapape, Tuauru R., 17° 32' 10" S. 149° 29' 15" W. alt. 50m. 09-vii-80, D.A. & R.E.G. Craig (1 ♂, BMNH; 1 ♂, BPBM; larvae, DSIR; 2 ♂, UASM; 2 ♂, USNM). Papenoo, Papenoo R., 17° 33' 15" S. 149° 25' 50" W. 22-x-28, A.M. Adamson (1 ♂, BMNH); 17° 36' 52" S. 149° 24' 51" W. 10-vii-80, D.A. & R.E.G. Craig (1 ♀, DSIR; 1 ♀, 3 ♂, MNHP; 4 ♂, UASM; karyotyped larvae, BMNH).

Tiarei, Fareteuira R., Cascades de Faarumai, 17° 32' 10" S. 149° 23' 48" W. 14-vii-80, 21-vii-80, D.A. & R.E.G. Craig (larvae, UASM). Onofea R., 17° 33' 30" S. 149° 23' 47" W. alt. 110 m. 14-vii-80, D.A. & R.E.G. Craig (larvae, UASM).

Mahaena, Mahape R., 17° 34' 00" S. 149° 20' 33" W. alt. 700 m 14-vii-80, D.A. & R.E.G. Craig (karyotyped larvae, BMNH).

Faaone, Utuofai R., 17° 39' 15" S. 149° 19' 00" W. 10-vii-73, D.A. & R.E.G. Craig (larvae, UASM).

Tautira, (Tahiti-iti), E. trib. Vaitepiha R., 17° 46' 30" S. 149° 15' 20" W. alt. 50 m. 19-vii-80, D.A. & R.E.G. Craig (1 ♀, 3 ♂, DSIR; larvae & pupae BMNH); Vaitepiha R., 17° 46' 30" S. 149° 10' 21" W. alt. 50m. 19-vii-80, D.A. & R.E.G. Craig.(3 ♀, CNCI; 1 ♂, DSIR; karyotyped larvae, BMNH; 1 ♂, larvae, UASM).

Teahupoo, (Tahiti-iti), Tiirahi R., 17° 51' 05" S. 149° 14' 15" W. 20-vii-80, D.A. & R.E.G. Craig (karyotyped larvae, BMNH; 3 ♀, 1 ♂, larvae, pupae, CNCI; 2 ♀, 2 ♂, larvae, pupae, DSIR; larvae and pupae UASM).

Paea, Ofaipapa, Robinson's Place, 02-iv-61, 28-iv-61, J.N. Belkin (larvae, USNM). Vaitiu R., 17° 34' 00" S. 149° 41' 22" W. 16-vii-74, D.A. & R.E.G. Craig (larvae, UASM).

Mataiea, Vaihiria R., (= Tahiria) 17° 44' 22" S. 149° 24' 15" W. alt. 80 m. 16-vii-80, (1 ♀, 1 ♂, DSIR; 1 ♀, larvae, UASM); 17° 41' 31" S. 149° 25' 02" W. alt. 250m. 17-vii-80, (1 ♀, larvae, pupae, BMNH; 1 ♀, 2 ♂, CNCI; 1 ♂, DSIR; 1 ♀, USNM; larvae, UASM), D.A. & R.E.G. Craig.

Mahaiatea, Taharuu R., 17° 42' 45" S. 149° 29' 15" W. alt. 135 m. 15-vii-80, D.A. & R.E.G. Craig (larvae, CNCI).

Punaauia, Punaruu R., 27-iv-1969, B. Hocking (larvae, UASM); 17° 38' 20" S. 149° 35' 40" W. 21-vi-73, 02-vii-73,

03-vii-73, 04-vii-73, (larvae, UASM); 17° 38' 20" S. 149° 35' 05" W. alt. 120m. 05-vii-73 (larvae, UASM), 06-vii-73 (larvae, UASM), 09-vii-73 (larvae, UASM), 05-vii-74 (larvae, UASM), 06-vii-74 (larvae, UASM), 08-vii-74 (larvae, UASM), 22-vii-74 (larvae, UASM), 07-vii-80 (2 ♂, BMNH; 1 ♀, MNHP; 1 ♀, 1 ♂, UASM) D.A. & R.E.G. Craig.

Simulium (Inseliellum.) "IIS"

Larvae of this cytospecies as identified by Rothfels (*in* Craig, 1983), cannot be morphologically separated from larvae of *S. tahitiense*. Possibly these larvae will eventually be shown to be those of *S. exasperans* (Rothfels, pers. comm., 1986), however, "IIS" is known only from Tahiti-iti.

Material Examined.— *Tautira*, (Tahiti-iti), Vaitepiha R., 17° 46' 30" S. 149° 10' 21" W. alt. 50 m. 19-vii-80, D.A. & R.E.G. Craig (5 karyotyped early instar larvae as slide mounts, DAC).

Remarks.— The material was taken with *S. tahitiense* larvae.

oviceps - group

Diagnosis.—
Pupa: scutellum rounded dorsally; with or without tubercles, if present, pointed; gill with dorsal filaments shorter, or subequal in length to others.
Larva: labral fans reduced; ray number small, rays short to almost absent; head spot pattern partially or completely negative; head margins prominently convex; postgenal cleft small to absent; head sensilla number normal or greatly increased; hypostomal teeth variable, from medial and lateral teeth sharp and prominent, to all teeth rounded and subequal in length, to median tooth with adjacent sublateral teeth short, or median tooth absent; posterior abdomen expanded abruptly laterally at segment VI, decreased in size more gradually posteriorly, or shape more normal. Anal sclerite with posteroventral arms extended partway, or virtually completely around posterior proleg. Anal papillae simple, with at most, only small accessory basal papillae.
Included taxa.— *S. castaneum* n. sp.; RAIATEA. *S. admixtum* n. sp., *S. arlecchinum* n. sp., *S. cataractarum* n. sp., *S. mesodontium* n. sp., *S. neoviceps* n. sp., *S. oviceps* Edwards and *Simulium* sp.; TAHITI.

Simulium (Inseliellum) admixtum n. sp.
(Figs. 36, 45)

Type.—
Holotype. Larva: penultimate instar; as slide mount; label data:-"Holotype", "Simulium (I.) admixtum Craig/ det D.A. Craig 1986", "Tahiti, Tiarei, Fareteuira R.,/ Cascades de Faarumai, /17° 32' 10" S. 149° 23' 48" W. /16-ii-83, D.A. Craig" (MNHP).
Specific epithet.— Named after the Greek word "admixtus" meaning "mixed", in reference to the unique suite of characters possessed by the single larva.
Diagnosis.—
Larva: head; sensilla numerous; spot pattern negative; median hypostomal tooth lacking; abdomen; cuticle with numerous, low ovoid tubercles.
Description.—
Adult Female. Unknown.
Adult Male. Unknown.

Pupa. Unknown.

Larva. Single penultimate instar larva; length 5.2 mm. Body: generally greyish with indistinct intersegmental regions. Head capsule: margins strongly convex posteriorly, as for *S. cataractarum* (Fig. 29); background colour pale with apices of corrugations dark brown; frontoclypeal apotome lighter anteriorly, darker posteriorly; anteromedian and posteromedian head spots negative, but barely so, posterolateral spots concolourous with surrounding darker brown; cervical sclerites fused to postocciput by narrow junction; stemmata surrounded by dark brown anterodorsally, narrow oblique clear posterodorsal region; cuticle with numerous lateral corrugations dorsally and ventrally; sensilla numerous with raised and strongly pigmented sockets, producing rugose appearance. Antenna: length 0.4 mm, just longer than labral fan stem, distal article length 0.1 mm. Labral fans: with 26 rays, nine lateral rays less substantial, *ca.* 0.6 mm. in length; microtrichia of median rays 0.50 times as long as ray width, pattern of long microtrichia interspersed between eight to 10 smaller microtrichia. Hypostoma (Fig. 36): median tooth lacking, four sublateral teeth per side, increasing slightly in length laterally, lateral teeth prominent, one paralateral tooth with steep base down to four lateral serrations, six hypostomal sensilla in row per side. Postgenal cleft: very shallow, broadly U-shaped, 5.0 times wider than deep. Postgenal bridge: 4.0 times longer than cleft. Mandible: apex (Fig. 45) with seven to nine spinous teeth extended almost to mandibular serration; serration as high as basal width, anterior edge longer than posterior, sensillum virtually absent from one mandible, double on other. Maxillary palpus: 3.5 times as long as width at base. Mandibular phragma: heavily pigmented, extended ventrad to 0.33 depth of maxilla base. Abdomen: segments I–IV of similar size, gradually increased in size to segment VIII; posteroventral tubercles situated laterally and very small; posterodorsal cuticle with clear, low ovoid tubercles and with trichoid sensilla, 16.0 μm long. Anal sclerite: with posteroventral arms 2.3 times longer than dorsolateral arms; pigment more distinct along anterior edges, sensillar sockets numerous and obvious. Circlet of hooks: 91 rows of hooks, 18–20 hooks per row. Anal papillae: simple, but each with very small basal papilla.

Bionomics.— The single larva was collected from the sheet of water flowing down the vertical rock face on the western side of the Cascade de Vaimahuta (Cascades de Faarumai), along with larvae of *S. cataractarum*, *S. oviceps* and *S. neoviceps*. Water temperature was 17° C. This temperature is relatively cool for simuliid localities in Tahiti.

Phylogenetic Relationships.— This species is similar in many respects to *S. cataractarum* in possessing strongly convex head margins, negative spots, lateral teeth of hypostoma longer than remainder of teeth and fused cervical sclerites. Eventual cytological examination of this species will probably show a close relationship. However, lack of the median hypostomal tooth (Fig. 36), and possession of two mandibular serrations on one mandible (Fig. 45), are unique.

Simulium (Inseliellum) arlecchinum n. sp.
(Figs. 27, 46)

Types.—

Holotype. Larva: mature last instar as slide mount; thorax used for scanning electron microscopy; hypostoma damaged; label data:- "Holotype", "Simulium (I.) arlecchinum Craig/ det/ D.A. Craig 1986", "Tahiti, Mataia, Vaihiria R.,/ 21-ii-84, P. Schröder" (MNHP).

Paratypes. Larvae: penultimate instars; as slide mounts; label data:- as for holotype (1, BMNH; 1, MNHP).

Specific epithet.— Based on the Italian word "arlecchino", meaning "harlequin" - in reference to the distinctive colour pattern on the ventral surface of the abdomen of the larvae.

Diagnosis.—

Larva: colour pattern on frontoclypeal apotome H-shaped; lateral hypostomal teeth prominent; abdomen with triangular pattern ventrally.

Description.—

Adult Female. Unknown.

Adult Male. Unknown.

Pupa. (Based on pharate material from holotype larva). Gill: length 0.9 mm; branching pattern normal, dorsal-most filament more than half as long as other filaments. Thorax: tubercles absent.

Larva. Last instar with dark pharate pupal gills; length 4.2 mm. Body: greyish-brown with pale narrow intersegmental regions. Head capsule (Fig. 27): margins generally parallel-sided; generally light brown; frontoclypeal apotome with broad

pale bands along ecdysial sutures; anteromedian and posteromedian head spots negative, H-shaped brown region surrounding muscle spots, extreme posteromedian region darker; cervical sclerites distinct; cuticle essentially smooth, corrugations normal; sensilla number normal. Antenna: slightly longer than labral fan stem, distal article length 0.8 mm, proximal article length 0.19 mm. Labral fans: with *ca.* 18 normal rays, 0.56 mm. in length, plus 13 smaller, less robust rays; microtrichia of medial rays up to 1.3 times longer than ray width, no microtrichial pattern. Hypostoma: essentially as for *S. tahitiense* (Fig. 44), but sublateral teeth slightly more prominent; six to eight hypostomal sensilla in row per side. Postgenal cleft: twice as wide as deep, sloping to slightly rounded vertex. Postgenal bridge: 3.0 times longer than cleft. Mandible: apex (Fig. 46) with ten spinous teeth extended essentially to mandibular serration; serration as high as basal width; proximal sensillum 0.50 height of serration. Maxillary palpus: 2.5 times as long as width at base. Mandibular phragma: extended ventrad to dorsal edge of maxillary base. Abdomen: segments I–III with triangular and diagonal pattern on sterna, less distinct on terga; posterior abdominal shape as for *S. cataractarum*; posteroventral tubercles placed laterally and not obvious; posterodorsal cuticle with ovoid, scale-like tubercles and with trichoid sensilla, 4.0 μm long. Anal sclerite: with posteroventral arms 1.4 times longer than dorsolateral arms; no lateral accessory sclerites. Circlet of hooks: 108 rows of hooks, 18–20 hooks per row. Anal papillae simple.

Bionomics.— Collected from grass trailing in the main stream of the unshaded, upper Vaihiria River, in fast, 5 cm deep water (P. Schröder, pers. comm., 1985).

Phylogenetic Relationships.— This species is placed in the *oviceps* - group on the basis of abdominal shape and negative head-spot pattern; however, head capsule and mouthpart structure are very similar to those of species in the *tahitiense* - group.

Simulium (Inseliellum) castaneum n. sp.
(Figs. 2, 28, 37, 47, 58, 60, 61)

Types.—

Holotype. Larva: slide mount; label data:- "Holotype", "Simulium (I.)/ castaneum Craig", "Society Islands, Raiatea, Temehani R., /1800', 1-ix-77, S.L. Montgomery,/ Bishop Museum Acc. #1977.361", "det. D.A. Craig 1986" (BPBM).

Paratypes. Adult: female; cleared and in vial; label data:- "Simulium (I.)/ castaneum Craig /det./ D. A. Craig 1986", "SOCIETY IS/ Raiatea, Uturoa,/ 0-100 m, III.1971.", "N.H.L. Krauss/ Collector/ BISHOP MUSEUM" (BPBM). Material in alcohol: one pupa, five last instar larvae, 10 penultimate larvae, twenty(+) earlier instar larvae; label data:- as for holotype (BPBM).

Specific epithet.— Based on the Greek word "castanea", meaning "brown", in reference to the generally even dark-brown of the larval head, labral fans, pupa and its cocoon.

Diagnosis.—

Larva: head uniformly dark brown; labral fan rays brown; hypostomal teeth very sharp.

Description.—

Adult Female. (From single specimen and immature pharate specimens). Body: generally black. Head: width 0.7 mm, depth 0.5 mm. Eyes: interocular distance 0.12 head width; frontal angle 86 degrees; ommatidia 0.01 mm in diameter, *ca.* 28 respectively across and up eye in middle row. Vertex: dark brown; vestiture of sparse dark brown hairs. Antennae: dark. Mouthparts: length, 0.33 head depth; mandibles, shorter than labrum, with *ca.* 14 minute teeth; lacinia with *ca.* 15–16 retrorse teeth; palpus, sensory vesicle 0.33 width of third article, opening 0.33 width of vesicle, *ca.* 10 sensillar sockets visible. Cibarial pump: space between proximal arms U-shaped, as wide as deep, smooth. Thorax: length 0.85 mm; scutum dark brown, shiny; scutellum lighter. Wing: length 1.7 mm, maximum width 0.8 mm. Legs: hind basitarsus parallel-sided, 7.5 times longer than wide; pretarsal claw smoothly curved with pointed apex, basal tooth 0.20 length of claw. Genitalia (Fig. 2): cercus bluntly cone- shaped in ventral view; hypogynial valves broadly rounded apically, extended to anal lobes, strongly diverged medially; stem of genital fork narrow, slightly swollen anteriorly, lateral triangular sclerites with blunt anterior apices; sternite VIII sclerotized medially, narrow posteriorly, widening anteriorly. Spermatheca: ovoid; pigmented; no pattern; clear area àt junction of sperm duct normal.

Adult Male. Unknown.

Pupa. Length: 2.8 mm, female. Gill: length 1.3 mm; branching pattern typical, dorsal-most filament 0.50–0.66 length of others. Thorax: tubercles absent, cuticle shiny. Abdomen: tergite I without hooks or spines; tergites II–IV with pronounced recurved hooks, those of tergite III smaller; tergites V and VI bare; tergites VII and VIII with very fine spine fields, those of tergite VIII stronger; sternite III clear; sternites IV–VII with anteriorly directed hooks, those of tergites IV

and V grouped close to midline, those of sternites VI and VII widely spaced; caudal spines very small. Cocoon: slipper-shaped, of medium weave; darkly coloured; covering pupa to base of gills,; anterior edge loosely woven, with spaces between threads.

Larva. Last instar larva with dark pharate pupal gills; length 6.2 mm. Body: evenly dark greyish-brown with thin lighter intersegmental regions. Head capsule (Fig. 28): relatively uniformly dark brown; posterolateral margins strongly convex; frontoclypeal apotome slightly lighter anteriorly, darker posteriorly; posteromedian and anterolateral head spot-two, negative, others positive; stemmata with darker area anteriorly, distinct lighter diagonal mark; cuticle with corrugations running laterally; sensilla numerous, with distinct raised sockets (Fig. 60); cervical sclerites fused to postocciput. Antenna: longer than labral fan stem, distal article length 0.14 mm, proximal articles length 0.34 mm, basal article very dark brown and longitudinally striated, medial article with irregular lighter patches, distal article uniformly light brown. Labral fans: with 29 dark brown rays, *ca.* 0.88 mm. in length, lateral four rays less substantial; microtrichia of all rays short, only 0.6 times as long as ray width, pattern of long microtrichia interspersed with five smaller microtrichia, very distinct (Fig. 58). Hypostoma (Fig. 37): teeth sharply pointed, median tooth prominent, five sublateral teeth per side, subequal in length, line of teeth tips sloping anteriorly to prominent lateral tooth longer than median tooth, one paralateral tooth, with steep base down to five or six lateral serrations; five or six hypostomal sensilla in row per side. Postgenal cleft: small, wider than deep, flat anteriorly. Postgenal bridge: 2.0 times longer than cleft. Mandible: apex (Fig. 47) with nine to 11 spinous teeth extended almost to mandibular serration; serration as high as basal width, length of sides subequal; proximal sensillum cone-shaped, on base of serration. Maxillary palpus: 3.1 times as long as width at base. Mandibular phragma: extended ventrad to 0.50 depth of maxilla base. Abdomen: segments increased gradually in size posteriorly to segment IV, then smoothly increased to maximum size at segment VII; posteroventral tubercles very small; posterodorsal cuticle with regular hemispherical tubercles and with trichoid sensilla, 15.0 μm long (Fig. 61). Anal sclerite: with posteroventral arms broad and continuous with lateral accessory sclerite extended to ventral surface, but not fused ventrally. Circlet of hooks: 106 rows of hooks, 14–16 hooks per row. Anal papillae: essentially simple; lateral papillae with one or two very small pointed basal papillae.

Bionomics.— Little is known about the habitat of this species. Larvae and pupae were taken from a cascade; a piece of grass was included with the material, but it is not known if the specimens were on vegetation.

Material Examined.— In addition to types I have seen the following: Two pupal cocoons and pieces of pupal exuviae, in alcohol, data as for holotype (BPBM).

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Simulium (Inseliellum) cataractarum n. sp.

(Figs. 3, 10, 24, 29, 38, 48, 64)

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Simulium "IS". Craig, 1983: 534. Schröder, 1985: 18.

Types.—

Holotype. Male: pinned; reared; emerging from pupa, with larval abdominal exuviae still attached; label data:- "Holotype", "♂", "Simulium (I.)/ cataractarum Craig/ det./ D.A. Craig 1986", "TAHITI, Mataiea, E. Lac Vaihiria,/ 17° 40' 58" S. 149° 24' 51" W. / alt. 480m. 22-vii-80, / D.A. Craig. Stat. #16." (MNHP).

Paratypes. Female: pinned; reared; pupal exuviae and cocoon as subsidiary material; head and genitalia in vial; label data as for holotype (MNHP). Females: pinned; reared; pupal exuviae and cocoons as subsidiary material; label data:- "TAHITI, Tiarei, Fareteuira R.,/ Cascade de Faarumai,/ 17° 32' 10" S. 149° 23' 28" W./ 17-ii-87, D.A. Craig. Stat. #15" (1 each, BPBM; BMNH; CNCI; DSIR; USNM; UASM). Male: pinned; reared; with pupal exuviae and cocoon as susidiary material; complete specimen cleared and in vial; label data as for holotype (MNHP). Male: pinned; reared; with pupal exuviae and cocoon as subsidiary material; head and genitalia in vial; label data as for holotype (BMNH). Males: pinned; reared; pupal exuviae and cocoons as subsidiary material; label data:- "TAHITI, Tiarei, Fareteuira R.,/ Cascade de Faarumai,/ 17° 32' 10" S. 149° 23' 28" W./ 17-ii-87, D.A. Craig. Stat. #15" (1 each, BPBM; BMNH; CNCI; DSIR; USNM; UASM). Pupa: (in alcohol), posterior larval exuviae still attached; label data as for holotype (BMNH). Larvae: in alcohol; label data as for holotype (9 penultimate, BMNH). Larvae: karyotyped; label data as for holotype (4,

BMNH; 3, BPBM; 4, MNHP). Larvae: in alcohol; locality data:- "Tiarei, Cascades de Faarumai, Fareteuira R., 17° 32' 10" S. 149° 24' 00" W. 20-vii-80, D.A.C." (8 last, MNHP). Larvae: penultimate; label data:-"Mataiea, E. Lac Vaihiria, /17° 40' 58" S. 149° 24' 51" W./ alt. 430m. 17-vii-80, /D.A. & R.E.G. Craig". (14, CNCI; 19, DSIR). Larvae: label data:- "Tiarei, immediately west of Trou du Souffleur, 17° 31' 30" S. 149° 23' 32" W. alt. 10m. 17-ii-87,/ D.A.C." (9 penultimate, DAC).

Specific epithet.— Named after the Latin word "cataracta" for "water fall", in reference to the cascades where larvae of this species are usually found.

Diagnosis.—

Pupa: gill with short dorsal filament; thoracic tubercles absent.

Larva: *oviceps* -type; head spot pattern negative; labral fan ray number reduced, rays pigmented medially; anal sclerite extended ventrally around anal proleg.

Recognition.— The holotype was chosen because the larval abdominal exuviae and the pupal exuviae provide definitive association to all stages. Larvae of *S. cataractarum* are very distinctive and it is quite suprising that they were not discovered previously. Included here for the present is the single karyotyped larval specimen designated *Simulium* "IS-complex" by Rothfels (*in* Craig, 1983). That specimen (DAC) is morphologically indistinguishable from larvae of *S. cataractarum*.

Description.—

Adult Female. Body: generally dark brown-black; length 1.7 mm. Head: width 0.6 mm, depth 0.3 mm. Eyes: interocular distance 0.6 times width of clypeus; frontal angle, 105 degrees; ommatidia 0.016 mm in diameter, *ca.* 33 and 37 respectively across and up eye in middle row. Post-ocular hairs: extended just to eye margin. Clypeus: pale, concolourous with ventral frons, as wide as deep; vestiture of substantial pale hairs. Antenna: total length 0.36 mm; scape, pedicel and base of first flagellomere yellowish, remaining flagellomeres light brown. Mouthparts: length, 0.33 head depth; mandibles, shorter than labrum with *ca.* 14 fine teeth; lacinia with 14–16 retrorse teeth; palpus, 0.5 mm long, distal article 0.2 mm long, third article with pronounced distomedial angle; sensory vesicle occupying 0.50 width of third article, opening 0.33 width of vesicle, *ca.* 20+ sensillar sockets visible. Cibarial pump: space between proximal arms smooth, U - shaped, as wide as deep. Thorax: length 0.9 mm; postpronotal lobe with tuft of yellow hair extended laterally beyond head margin; scutum uniformly blackish brown, anterolateral margins lighter, vestiture of substantial pale hairs; scutellum with distinctly concave posterolateral edges, vestiture of pale golden and dark hairs meeting medially; postscutellum concolourous with abdomen; pleuron brown; mesepimeral tuft of hairs golden. Wing: length 1.6 mm, maximum width 0.8 mm: veins pale yellow; stem vein hair tuft sparse; basicosta with darker hairs, remainder of costa with spines and hairs. Halter: pale. Legs: foreleg light brown; fore-femur 0.63 mm long; fore-basitarsus 6.0 times as long as wide, tarsomeres dark brown: meso- and metatrochanter dark brown, distal quarters of meso-femur and tibia darker brown; basitarsus darker brown on distal 0.33; hind basitarsus parallel-sided, 6.0 times longer than wide, distal tarsomere squarish; pretarsal claw slender, gently curved with sharp apex, basal tooth 0.50–0.66 length of claw. Abdomen: generally dark brown; basal fringe of pale yellow hairs extended to abdominal segment II; tergites not distinct, vestiture of tergites I–VI of pale shiny hairs, those of tergites VII–IX darker; pleural regions concolourous with tergum; sternites paler. Genitalia (Fig. 3): cercus, bluntly rounded in ventral view; hypogynial valves extended to anal lobe, medial margins slightly concave, converging posteriorly, broadly rounded posteriorly; stem of genital fork smooth, lateral arms broad, lateral sclerite large, with apex anteriorly-directed, sharply angulate; sternite VIII pigmented region broadly dome-shaped. Spermatheca: ovoid; slight reticulate pattern; not heavily pigmented; clear area at junction of sperm duct large.

Adult Male. Body: generally blackish-brown; length 1.7 mm. Head: width 0.5 mm, depth 0.4 mm. Eyes: upper ommatidia 0.03 mm in diameter, 19 and 22 respectively up and across middle rows; lower ommatidia 0.01 mm in diameter, eight and 12 respectively up and across middle rows. Labrum: pale. Clypeus: narrow dorsally, widening ventrally, 0.20 as wide as head. Antenna: length 0.4 mm; pedicel and scape slightly lighter in colour than flagellum; pilose. Mouthparts: 0.25 length of head depth; mandibles insubstantial, three very small apical teeth; lacinia hairy, without retrorse teeth; palpus 0.29 mm long, distal article 0.27 mm, sensory vesicle occupying only 0.50 of width of third palpal article, opening less than 0.33 width of vesicle, eight to 10 sensillar sockets visible. Thorax: length 0.24 mm; postpronotal lobe with small tuft of golden hairs; scutum black, vestiture of golden hairs, longer posteriorly; scutellum pale yellow, posterior edges slightly concave in dorsal view, vestiture of lateral golden hairs; postscutellum dark, dull brown. Wing: length 1.5 mm, maximum width 0.7 mm; veins pale; stem vein dark, hair tuft black, substantial. Halter: yellowish. Legs: coxae shiny brown; fore-femur with yellow medial area; middle and hind femurs similar, vestiture of long dark hairs; tibiae dark on posterior margin, fore basitarsus parallel sided, but expanded slightly distally, 5.0 times longer than wide; fore tibia 7.0 times as long as wide; pretarsal claw smoothly curved, *ca.* 22 grappling hooks. Abdomen: generally blackish-brown; basal fringe of yellow hairs extended to abdominal segment III; tergite II yellow anteriorly; tergites I–VI with vestiture of golden hairs,

that on tergites VII and VIII darker; pleuron mottled brown; sternites III pale yellow laterally, squarish. Genitalia (Fig. 10): gonocoxa *ca.* 2.0 times as long as basal width; gonostylus *ca.* 0.33 as wide as long, strongly curved with one blunt terminal spine, as long as wide; ventral plate with posterior apex broadly rounded, hairy, posterolaterally slightly concave, broadly angulate, anterior arms heavily sclerotized and angulate, anteromedian notch distinct.

Pupa. Length 1.9–2.6 mm. Gill: length 1.4–2.0 mm; branching pattern typical, dorsal-most filament 0.33–0.50 length of other filament, occasionally reflexed posteriorly over thorax. Thorax: cuticle clear, brown; tubercles absent. Abdomen: tergite I–III bare; tergites IV and V with hooks; caudal spines very short, but distinct. Cocoon: slipper-shaped.

Larva. Last instar with dark pharate pupal gills; length 4.3–5.3 mm. Body: greyish-brown, with slightly paler intersegmental regions. Head capsule (Fig. 29): generally rich brown; margins convex, widest at 0.33 length from posterior of capsule (Fig. 64); frontoclypeal apotome brown anteriorly; head spots negative, surrounded by darker area; cuticle slightly rugose, with corrugations; sensilla numerous; cervical sclerites distinct, but fused to occiput; Antenna: slightly shorter than labral fan stem; length 0.38 mm; distal article 0.13 mm long, proximal article darker than head capsule, other articles lighter; base pigmented. Labral fans: with 12–15 robust brown rays *ca.* 0.8 mm. in length, plus three to five thinner, smaller medial rays; each ray with median dark brown patch; microtrichia of rays 0.50 as long as ray width, no microtrichial pattern. Hypostoma (Fig. 38): flexed dorsally; median tooth rounded, not protruding beyond prominent lateral teeth; five sublateral teeth per side increasing in size slightly to prominent lateral teeth; one small paralateral tooth; six lateral serrations; five to six hypostomal sensilla in row per side. Postgenal cleft: small, U-shaped, twice as wide as deep. Postgenal bridge: 2.5 times as long as cleft (Fig. 29). Mandible: apex (Fig. 48) with 16 to 20 spinous teeth, decreased rapidly in size posteriorly, extended almost to mandibular serration; serration prominent, as high as basal width, anterior edge twice as long as posterior edge, basal sensillum minute and on serration base, heavily pigmented. Maxillary palpus: 4.1 times as long as width at base. Mandibular phragma: heavily pigmented and substantial, extended ventrad to 0.50 depth of maxillary base. Abdomen: segments increased gradually in size to segment V where a sudden lateral increase in size occurs (not as prominent as in *S. oviceps*); posteroventral tubercles prominent (Fig. 24); posterodorsal cuticle smooth, with numerous trichoid sensilla 11.0–22.0 μm long. Anal sclerite: with median portion broad, deeply pigmented: sensillar sockets showing clearly; anterodorsal arms with small lateral extension; posteroventral arms continuous with lateral accessory sclerites, extended, or almost, completely around posterior proleg. Circlet of hooks: 108 rows of hooks, 15–17 hooks per row. Anal papillae: simple.

Bionomics.— A typical habitat for larvae of this species, such as at the Cascades de Faarumai (= La Trois Cascades) and at Lac Vaihiria, consists of thin sheets and trickles of water flowing over hard rock. At Cascades de Faarumai, larvae were on the rock face, on filamentous algae, leaves of macrophytes and dead leaves blown onto the rock face. The Cascades de Faarumai (Vaimahuta Cascade) site is of spring origin, arising from a horizontal crack two-thirds of the way up, and to the right of the main falls. On the 17-ii-1987 suspended particulate material larger than 0.45 μm in the water was 6.9 mg/litre. That in the main cascade was 3.0 mg/litre. This difference is suprising, because the spring-fed flow over the rock was expected to have less particulate material. Examination of the filters, showed that diatoms were the dominant material in the spring-fed flow. Whether this is significant for evolution of the species which occupy this habitat is not known. The pH was 8.2. Water temperatures ranged from 17–23° C. The origin of the Lac Vaihiria cascade is not known, but water temperature was 20° C.

Simulium cataractarum is clearly a torrenticolous species. Schröder (1985) has collected *S. cataractarum* larvae from cascades in the Maruia, Taharuu and Tuauru Valleys, and in the Potiai and Vaihiria Rivers. A particulary important site for this species is the small cascade west of le Trou du Souffleur. Here, *S. cataractarum* larvae only are found in a small cascade above the circum-island road, but immediately above that, where the stream flattens out, only *S. malardei* larvae are found. This unique situation may allow determination of habitat requirements for the two species. Schröder (1985, 1988) notes that larvae of *S. cataractarum* have lower selectivity for small algae than do larvae of *S. tahitiense*.

Larvae of *S. cataractarum*, along with those of *S. neoviceps* and some of those of *S. oviceps*, have countercoloured body pigmentation, *i.e.,* with the dorsal surface much darker than the pale ventral surface. Presumably this is to blend into the dark basaltic rock substrate. Whether this is an adaptation to avoid predation, or for protection from intense solar radiation is not known.

Material Examined.— In addition to types, I have seen the following:

Tiarei, Fareteuira R., Cascades de Faarumai, 17° 32' 10" S. 149° 23' 28" W. 30-vi-80, 14-vii-80, 20-vii-80, 21-vii-80, 02-vii-81, 11-ii-83, 16-ii-83, D. A. & R.E.G. Craig (larvae, DAC).
Teahupoo, (Tahiti-iti), cascade below Mt. Arope, alt. 30 m. 22-iii-84, P. Schröder (small, early instar larvae, DAC).
Paea, Grotte de Mara, 17° 44' 48" S. 149° 34' 10" W. 00-00-74, D.A. Craig (2 larvae, DAC).

Simulium (Inseliellum) mesodontium n. sp.
(Figs. 41, 52, 63)

Type.—

Holotype. Larva: mature last instar; as slide mount; label data:- "Holotype", "Tahiti, Tiarei, Cascades de Faarumai, /Fareteuira R., 17° 32' 10" S. 149° 23' 48" W./ 14-vii-80, D.A. Craig." (MNHP).

Specific epithet.— Named after the Greek words "mesos" for "middle", and "odontos" for "tooth" in reference to the prominent median tooth of the hypostoma.

Diagnosis.—

Larva: hypostoma with sublateral teeth laterad of median tooth small; abdomen covered with ovoid tubercles.

Description.—
Adult Female. Unknown.
Adult Male. Unknown.
Pupa. Based on pharate material from last instar larva. Thorax: tubercles absent. Gill: length 1.2 mm; branching pattern normal, dorsal-most filaments equal in length, slightly longer than 0.50 length of longest other filament.
Larva. (Single carcase remaining from karyotyping). Last instar with dark pharate pupal gills; length 4.0 mm. Body: generally light brownish-grey with slightly lighter intersegmental regions. Head capsule: pattern as for *S. oviceps*; sensilla numerous; cervical sclerites fused to postocciput. Hypostoma (Fig. 41): with two main lateral lobes, separated by large median tooth and two small sublateral teeth; other sublateral teeth increased smoothly in size out to lateral tooth and single paralateral tooth; lateral serrations absent; five hypostomal sensilla grouped per side. Postgenal cleft: very small, V-shaped. Postgenal bridge: 5.0 times longer than cleft. Mandible: apex (Fig. 52) with 13 fine spinous teeth extended to base of mandibular serration, apical teeth rounded; serration wider at base than high; sensillum small and closely applied to serration. Abdomen: as for *S. oviceps*; posteroventral tubercles absent; posterodorsal cuticle with raised, closely packed, lightly pigmented, ovoid tubercles, 18 μm long, tubercles evenly distributed over dorsal surface of abdomen, smaller on prothoracic dorsum, absent from ventral cuticle; and with trichoid sensilla, 22.0 μm long (Fig. 63). Anal sclerite: with anterodorsal arms longer than normal; posteroventral arms thin, fused to accessory sclerite, extended around anal proleg, not fused ventrally. Circlet of hooks: 96 rows of hooks, 15–17 hooks per row. Anal papillae: simple; each with small basal papilla.

Bionomics.— Gut contents appear normal as for typical filter feeding larvae, so no special function can be assigned to the aberrant median tooth of the hypostoma.

Phylogenetic relationships.— Head, labral fan structure and body shape of the larva place this species firmly in the *oviceps* - group. Karyotypic examination of the specimen provisionally identified it as *S. oviceps* (Rothfels, pers. comm. 1984), but morphologically it is clearly a separate species.

Simulium (Inseliellum) neoviceps n. sp.
(Figs. 32, 53, 67, 68)

Simulium "neooviceps". Craig, 1983: 534.

Types.—

Holotype. Larva: penultimate instar; in alcohol; label data:- "Holotype", "Tiarei, Fareteuira R., Cascade de Faarumai,/ 17° 32' 10" S. 149° 24' 00" W. 18-ii-87", "Simulium (I.) neoviceps Craig/ det/ D. A. Craig 1987" (MNHP).

Paratypes. Larva: penultimate instar; as slide mount; label data:- "Tahiti, Mataiea, E. Lac Vaihiria,/ 17° 40' 58" S. 149° 24' 51" W. alt. 480m. /16-vii-80. D.A. & R.E.G. Craig." (MNHP).

Larva: penultimate instar; as slide mount; label data:- "Paea, Grotte de Mara, /17° 44' 48" S. 149° 33' 48" W. /alt. 10m. 1974, D.A. Craig," (MNHP). Larvae: in alcohol; label data as for holotype (1, BMNH; 2, BPBM; 2, DAC; 1, MNHP).

Specific epithet.— Named after the Greek word "neos" meaning "new" and "oviceps", from *S. oviceps*, in reference to this species' similarity to *S. oviceps*.

Diagnosis.—

Larva: labral fans highly reduced, virtually absent; hypostoma protruding anteriorly; anal sclerite extended ventrally around posterior proleg.

Recognition.— Although *S. neoviceps* is quite distinct morphologically and cytologically from *S. oviceps* (Rothfels *in* Craig, 1983) by virtual absence of labral fans, extent of the posteroventral arms of the anal sclerite around the anal proleg and number of head sensilla (or hairiness), some larvae presently assigned to *S. oviceps* have very small labral fans and may be mistaken for those of *S. neoviceps*.

Description.—

Adult Female. Unknown.

Adult Male. Unknown.

Pupa. Unknown.

Larva. Similar to *S. oviceps*, but differing in the following characters:- Head: spot colour pattern negative, but not distinctly so medially (Figs. 32, 67); cuticle essentially smooth; sensillar number normal. Antenna: much longer than cephalic fan stem, length 0.18 mm; distal article length 0.07 mm; proximal articles darker, concolourous. Labrum: cone-shaped; labral fans (Figs. 67, 68) highly reduced with only four longer rays; *ca.* 0.04 mm in length, plus two very short rays; microtrichia as long as ray width. Hypostoma: extending anterior of head capsule lateral margins; teeth as for *S. oviceps*, six to seven hypostomal sensilla per side, tightly grouped. Mandible: apex (Fig. 53.) with seven spinous teeth extended to serration; serration small, as high as wide; sensillum separate from serration. Abdomen: shape as for *S. oviceps*; posteroventral tubercles distinct. Anal sclerite: extended completely around anal proleg; fused ventrally. Circlet of hooks: 86 rows of hooks, 16–18 hooks per row. Anal papillae: simple.

Bionomics.— The habitat for larvae of this species is perhaps the most extreme of all Tahitian simuliid habitats. In the Cascades de Faarumai, larvae were taken from the right of the main falls where water was flowing in a thin sheet down vertical bare rock. Larvae probably do not filter feed, since the labral fans are so small. Browsing feeding behaviour is suggested from examination of gut contents which showed many pieces of fine inorganic material, and by the rounded and broken hypostomal teeth in specimens ready to moult. Recently ecdysed individuals had sharp hypostomal teeth, as do *S. oviceps* (Craig, 1975a). No other simuliid species were taken from that particular site. A few meters closer to the main falls where filamentous algae grew on the rocks, both *S. cataractarum* and *S. oviceps* were collected, similar to the situation at the Lac Vaihiria site.

Phylogenetic relationships.— The morphological convergences in *S. neoviceps* and *S. oviceps* larvae to those of the browsing simuliid *Gymnopais* is startling. The body shape, to allow the abdomen to bend so that the mouthparts can be applied to the substrate (Craig, 1977); the reduction of the labral fan with concomitant reduction in size of the labrum (Craig, 1974); the reduction in the size of postgenal cleft, probably for strengthening the head; the shortening of the mandible and reduction of apical teeth for scraping the substrate; and flattening of the hypostomal teeth and extension of the hypostoma anteriorly for the "pan and broom" technique of feeding (Currie and Craig, 1987), have been independently developed in both groups.

Material Examined.— In addition to types I have seen the following: *Tiarei*, Fareteuira R., Cascade de Faarumai, 17° 32 ' 10" S. 149° 23 ' 48" W. 16-ii-83, D.A. Craig (SEM specimen, DAC). Larvae: two destroyed during karyotyping.

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Simulium (Inseliellum) oviceps Edwards
(Figs. 8, 15, 20, 25, 34, 43, 55, 66, 70)

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Simulium oviceps Edwards 1933: 37, 1935: 37. Lectotype larva (by present designation), TAHITI. Smart, 1945: 511. Grenier and Rageau, 1960: 734. Grenier and Rageau, 1961b: 174. Dumbleton, 1962: 77. Davies, 1965: 172. Rubtsov, 1974: 242, 244. Craig, 1975a: 466. Craig, 1975b: 299. Crosskey, 1981: 8, 61. Craig, 1983: 533. Schröder, 1985: 17.
Inseliellum oviceps (Edwards). Rubtsov, 1974: 275.
Simulium (Inseliellum) oviceps Edwards. Crosskey, 1987: 388.

Types.—

Lectotype. By designation from syntype series. Larva: slide mount; label data:- "625 TYPE 625,/ Simulium oviceps Edw./ Papara River, Tahiti,/ Mumford and Adamson" (BPBM).

Paralectotypes. Adults: pinned; on acetate; label data:- "Paralectotype", "Syntype", "Simulium (I.) oviceps Edw./ det. /D.A. Craig 1986", "Tahiti, Tautira. /9.viii.1925. /Miss Cheesman./ B.M. 1925. 392", "Syntype" (2 ♀, BMNH). Adult: pinned; on acetate; label data:- "Paralectotype", "Syntype", "Simulium (I.) oviceps Edw./ det. /D.A. Craig 1986", "Society Is. Tahiti. /16.3.25 L. E. Cheesman. /B. M. 1925 - 464", "Syntype" (1 ♀, BMNH). Adult: pinned; label data:- "Paralectotype", "Syntype", "Simulium (I.) oviceps Edw./ det./ D.A. Craig 1986", "Tahiti", "Society Is. 500 '. /Tahiti I.", "Faraura Val. /11-17-28", "Hitiaa 11-17-28", "5 miles from sea", "A.M. Adamson Collector", "Pacific Entomological Survey", "Brit. Mus. 1931.234", "? oviceps" (1 ♀, BMNH). Adult: pinned; label data:- "Society Is. Tahiti I", "Faraura Val. 12-20-28", "Hitiaa 500", "5 miles from sea", "Mumford & Adamson", "Pacific Entomological Survey", "Brit. Mus. 1931-234", "Syntype", "Paralectotype", "Simulium (I.) oviceps Edw./ det. /D.A. Craig 1986" (1 ♀, BMNH). Adult: pinned; label data:- "Society Is. / 1000 ' Tahiti I", "Fautaua Val. / 8-23-28", "NR VANILLA PLANT", "SIMULIUM", "A.M.Adamson collector", "Pacific Entomological Survey", "Brit. Mus. 1931-234", "Syntype", "Paralectotype", "Simulium (I.) oviceps Edw./ det./ D.A. Craig 1986" (1 ♀, BMNH). Adult: pinned; label data:- "Society Is. / 1000 ' Tahiti I", "Fautaua Val. / viii-22-28", "NR VANILLA PLANT", "SIMULIUM", "A.M. Adamson collector", "Pacific Entomological Survey", "Brit. Mus. 1931-234", "Syntype", "Paralectotype", "Simulium (I.) oviceps Edw./ det. /D.A. Craig 1986" (1 ♀, BMNH). Adult: pinned; label data:- "Society Is. /150m Tahiti I", "Papenoo Val /xi-9-28", "A.M. Adamson Collector", "Pacific Entomological Survey", "Brit. Mus. 1931-234", "Syntype", "Paralectotype", "Simulium (I.) oviceps Edw./ det./ D.A. Craig 1986" (1 ♀, BMNH). Adult: pinned; label data:- "Society Is. /150m Tahiti I", "Papenoo Val /10-23-28", "10 kilo from sea", "A.M. Adamson Collector", "Pacific Entomological Survey", "Syntype", "Paralectotype", "Simulium (I.) oviceps Edw./ det./D.A. Craig 1986" (1 ♀, BMNH). Adult: pinned; label data:- "Society Is. /150m Tahiti I", "Tipaerui Val /ix-12-28", "3 miles from sea", "A.M. Adamson Collector", "Pacific Entomological Survey", "Syntype", "Paralectotype", "Simulium (I.) oviceps Edw./ det. /D.A. Craig 1986" (1 ♀, BMNH).

Diagnosis.—

Pupa: dorsal gill filament short or long; thoracic tubercles pointed.

Larva: reduced labral fans; head sensilla numerous; laterally expanded posterior abdomen.

Recognition.— Included for the present in this species are larvae which have even smaller labral fans with fewer rays. These larvae have the arms of the anal sclerite further extended around the anal proleg.

Description.—

Adult Female. Body: colour variable, generally black to light brown; length 1.2–1.5 mm. Head: black-brown; width 0.36–0.41 mm, depth 0.25–0.36 mm. Eyes: interocular distance 0.12 width of head.; frontal angle 85 degrees; ommatidia 0.013 mm in diameter, *ca.* 28 and 30 respectively across and up eye in middle row. Vertex: black with vestiture of concolorous hairs. Frons: black-brown. Clypeus: concolorous with frons, pale ventrally; finely pilose; slight medial projection. Antenna: length 0.25 mm; evenly dark brown. Mouthparts: length less than 0.50 head depth; mandibles as long as labrum, *ca.* 15 small teeth; lacinia with *ca.* 15 retrorse teeth; palpus, 0.88 mm long, distal article 0.19 mm long, proximal article concolorous with clypeus, sensory vesicle occupying 0.50 width of third article, opening 0.33 width of vesicle, *ca.* 10 sensillar sockets visible. Cibarial pump: space between proximal arms U-shaped, smooth, as wide as deep. Thorax: length 0.52–0.63 mm; postpronotal lobe with tuft of hairs paler than scutum; scutum evenly dark brown, slightly shiny, vestiture of short, slightly golden hairs; scutellum apex sharp, posterolateral sides concave, forming generally obtuse angle, pale to concolorous with scutum, vestiture of sparse black hairs; postscutellum, concolorous with scutellum; pleuron dark brown. Wing: length 1.1–1.4 mm, maximum width 0.53–0.58 mm; stem vein hair tuft variable, from sparse to almost absent; basicostal vein with few hairs. Halter: pale. Legs: generally evenly brown; pretarsal claw smoothly curved with sharp apex; basal tooth 0.50 length of claw, diverging from claw. Abdomen: light brown to dark brown; basal fringe of sparse hairs extended to posterior of segment II. Abdomen: tergites I and II as wide as abdomen; tergites III–VI narrower anteriorly, expanded posteriorly, occasionally subshining; pleural regions pilose; sternum slightly mottled; sternites I–IV not apparent; sternites VI and VII narrow anteriorly, expanded posteriorly. Genitalia (Fig. 8.): cercus in lateral view slightly curved dorsally and ventrally with sharp apex; hypogynial valves with dark edges medially, pale apically, broadly rounded posteriorly extended just beyond base of anal lobe; stem of genital fork smooth, long, lateral sclerites triangular with anterior apex sharply angulate, laterally concave. Spermatheca: ovoid; slight pattern of longitudinal striations; not heavily pigmented; clear area at junction of sperm duct normal.

Adult Male. Body: generally black; length 1.1–1.4 mm. Head: width 0.44–0.50 mm, depth 0.34–0.39 mm. Eyes: upper ommatidia 0.02 mm in diameter, 16 and 14, respectively up and across eye; lower ommatidia, 0.01 mm in diameter. Frons: shiny black-brown, 0.33 head width. Clypeus: 0.25 as wide as head. Antenna: length 0.24 mm, uniformly dark brown. Mouthparts: 0.20 length of head depth; mandibles with fine hair-like teeth apically; lacinia lacking retrorse teeth, but with fine hairs apically; palpus 0.19 mm long, sensory vesicle spherical, occupying only 0.33 of width of third palpal article, opening less than 0.33 width of vesicle, *ca.* nine sensillar sockets visible. Thorax: length 0.41–0.55 mm; scutum velvety black brown, vestiture of short golden hairs; postpronotal lobe lighter with small tuft of hairs; scutellum cone-shaped in dorsal view, apex pronounced and pale with vestiture of sparse, black hairs; postscutellum dark brown, medial black area; pleuron brown. Wing: length 1.1–1.2 mm, maximum width 0.5–0.6 mm, stem vein hair tuft of few, but substantial hairs. Halter: greyish. Legs: generally brown, with black vestiture; pedisulcus distinct; pretarsal claw slightly curved; *ca.* 22 grappling hooks. Abdomen: jet black; vestiture of sparse black hairs; basal fringe of dark hairs extended to segment III. Genitalia (Fig. 15): gonocoxa 1.0–1.2 times as long as basal width; gonostylus approximately 2.0 times as long as basal width, strongly curved with one large blunt terminal spine; ventral plate hairy medially, broadly rounded posteriorly, slightly concave laterally, anterior sclerotized arms pointed, anteromedian notch very distinct and rounded.

Pupa. Length; 1.3–1.6 mm male; 1.3–1.9 mm female. Gill (Fig. 20): length, 0.8–0.9 mm male, 0.56–1.0 mm female; branching pattern typical, dorsal filament 0.25–0.75 length of other filament, occasionally as long, or very short, or absent, variable even on same specimen. Thorax: tubercles pointed (Fig. 70); sternites and tergites as for *S. exasperans*.

Larva. Last instar with dark pharate pupal gills; length 2.7–3.8 mm. Body: greyish-brown with narrow pale anterior intersegmental regions; ventrally pale, dorsal colour occasionally extended completely around abdominal segment I. Head capsule (Figs. 34, 66): variable, generally rich brown, but may be pale ventrally; frontoclypeal apotome pale anteriorly and laterally, posteriorly to stemmata, light brown medially, brown posteriorly; shape, narrow anteriorly, widest opposite stemmata, narrowing rapidly to parallel sided (variable – may be narrowest just posterior to stemmata, widening slightly posteriorly); spot pattern negative; stemmata with clear area posterolaterally, occasionally with narrow curved mark dorsally; cervical sclerites fused to head capsule; sensillae numerous (Fig. 66). Antenna: 3.0 times longer than labral fan stem, length 0.14 mm, distal article 0.06 mm; antennal phragma extensive and heavily pigmented. Labral fans: reduced; stem small, but distinct; eight to 12 short rays, *ca.* 0.17 mm in length; microtrichia of medial rays as long as ray width, pattern of longer microtrichia interspersed with seven or eight smaller microtrichia. Hypostoma (Fig. 43): all teeth similar and forming slightly convex line, median tooth protruding slightly; depending on age of larva, wear may be apparent on sublateral teeth; two paralateral teeth; two or three small lateral serrations; four or five grouped hypostomal sensilla per side; hypostoma produced anteriorly from head capsule. Postgenal cleft: rounded, as wide as deep, irregular anteriorly. Postgenal bridge: 3.0 times length of cleft. Mandible: short and curved, apex (Fig. 55) with blunt apical teeth of similar length (depending on age of larva), seven or eight spinous teeth extended to mandibular serration; serration as high as basal width, sharply pointed and curved posteriorly; sensillum more than 0.50 height of serration, similarly shaped. Maxillary palpus: 2.0 times as long as width at base. Mandibular phragma: strongly pigmented, extended ventrad to 0.50 depth of maxilla base. Abdomen: segments I to IV of similar size, segment V increased in size rapidly laterally to maximum size at segment VI; segments I–IV, constricted at intersegmental region, giving corrugated appearance to abdomen; posteroventral tubercles prominent; posterodorsal cuticle essentially smooth, with bifurcate sensilla, 8.4 μm long. Anal sclerite; with posteroventral arms 2.2 times longer than dorsolateral arms, expanded ventrally; separate lateral accessory sclerites absent. Circlet of hooks; 91 rows of hooks, 13–14 hooks per row. Anal papillae: variable; two or three basal tubercles on each papilla, ranging in size from small to as long as papilla (Fig. 25).

Bionomics.— *Simulium oviceps* is the second most common simuliid on Tahiti, occurring sympatrically with *S. tahitiense* in most of its habitats. *Simulium oviceps* has always commanded the most interest of all the Tahitian simuliids, because of the highly reduced labral fans of the larvae (Dumbleton, 1962; Davies, 1974; Craig, 1974; 1975 a, b). I had suggested (Craig, 1975a), that *S. oviceps* larvae were browsers because of the particles of volcanic glass in their guts. That was corroborated by observations on feeding behaviour (Craig, 1977). Schröder (1985) found a higher proportion of ingested detritus particles in *S. oviceps* larvae than in associated *S. tahitiense* larvae.

In the larger rivers, larvae of *S. oviceps* tend to be found around the outside of the dense aggregations of *S. tahitiense* which are normally found under large rocks in strong flow. Elsewhere, *S. oviceps* larvae and pupae can be found in deep depressions in the volcanic boulders, or on the smooth rock of cascades, or occasionally on filamentous algae. Although nowhere nearly as abundant as larvae of *S. tahitiense*, those of *S. oviceps* can be numerous and form monospecific populations. At Bain Loti (19-ii-1987), a full range of larval instars and pupae, were collected from dead leaves, and in particular, from plastic bags (garbage) in the water. Particulate matter larger than 0.45 μm, in the water at that time, was 8.3 mg/litre. The pH was 8.3 and the temperature 23° C.

Phylogenetic Relationships.— *S. oviceps* as presently described is probably a complex of species. Larvae taken with *S. tahitiense* from the larger rivers are morphologically very consistent. However, some larvae from the Cascades de Faarumai and the Vaihiria River possess labral fans intermediate in size between *S. oviceps* and *S. neoviceps*, and the anal sclerite posteroventral arms extend well around the anal proleg. Further material and karyological examination of that form is needed.

Material Examined.— In addition to types, I have seen the following:

Adults: pinned:

Tahiti, Faraura Val. 11-17-28, 11-17-28, 5 miles from sea, A.M. Adamson Collector, Pacific Entomological Survey, Brit. Mus. 1931.234, Simulium (I) oviceps /det./ D.A. Craig 1986 (1 ♀, BMNH).

Papeete, Fautaua R., Bain Loti, 17° 33' 15" S. 149° 33' 00" W. 19-ii-87, D.A. Craig. (2 ♂, DSIR; 2 ♂, 1 ♀, MNHP; 4 ♂, BPBM; 2 ♂, 2 ♀, USNM)

Haapape, Tuauru R., 17° 32' 10" S. 149° 29' 15" W. alt. 50 m. 09-vii-80, D.A. & R.E.G. Craig. Stat. #3 (2 ♂, BMNH; 2 ♂, MNHP).

Papenoo, Society Is. 150 m. Tahiti I., Papenoo Val. 10-27-28, 10 kilo. from sea, in cop., A.M. Adamson Collector, Pacific Entomological Survey, Brit. Mus. 1931.231, ? oviceps, (specimens now cleared and in vial) (1 ♂, 1 ♀, in cop., BMNH). Papenoo R., 17° 36' 52" S. 149° 24' 51" W. 10-vii-80, D.A. & R.E.G. Craig (1 ♂, BPBM; 1 ♂, 1 ♀, CNCI; 4 ♂, DSIR; 2 ♂, UASM).

Tautira, (Tahiti-iti), Vaitepiha R., 17° 46' 30" S. 149° 10' 21" W. alt. 50 m. 19-vii-80, D.A. & R.E.G. Craig. Stat.#13 (1 ♀, 1 ♂, BPBM).

Teahupoo, (Tahiti-iti), Tiirahi R., 17° 51' 05" S. 149° 14' 15" W. 20-vii-80, D.A. & R.E.G. Craig (2 ♀, 1 ♂, DAC; 2 ♂, DSIR; 1 ♂, UASM).

Mataiea, Aug. 1928. A. Tonnoir. BM. 1930.513, ?oviceps (1 ♂, BMNH). Vaihiria R., 17° 44' 22" S. 149° 24' 15" W. alt. 80m. 16-vii-80, D.A. & R.E.G. Craig (1 ♂, CNCI).

Punaauia, Punaruu R., 17° 38' 20" S. 149° 35' 05" W. alt. 120m. 07-vii-80, D.A. & R.E.G. Craig (1 ♀, cleared in vial, BMNH; 1 ♀, MNHP; 1 ♀, UASM).

Alcohol material:-

Papeete, Fautaua R., Bain Loti, 17° 33' 15" S. 149° 33' 00" W. 08-vii-74 (larvae, DSIR), 15-vii-74 (larvae, pupa, BMNH); 16-vii-74 (larvae, BMNH); 08-vii-80, (larvae CNCI; larvae, pupae, USNM); 01-vii-81 (larvae, pupa, CNCI; larvae, DAC), D.A. & R.E.G. Craig.

Haapape, Tuauru R., 17° 32' 10" S. 149° 29' 15" W. alt. 50m. 09-vii-80, D.A. & R.E.G. Craig (pupa, DAC; larvae, MNHP).

Papenoo, Papenoo R., 17° 36' 52" S. 149° 24' 51" W. 10-vii-80, D.A. & R.E.G. Craig (larvae, CNCI).

Tiarei, Fareteuira R., Cascades de Faarumai, 17° 32' 10" S. 149° 24' 00" W. 16-ii-83, (larvae, MNHP); 17-ii-87 (larvae, DAC) D.A. Craig .

Mahaena, Mahape R., 17° 33' 00" S. 149° 20' 33" W. 14-vii-80, alt. 700m. D.A. & R.E.G. Craig (karyotyped larvae, BPBM; larvae, DAC).

Tautira, (Tahiti-iti), Vaitepiha R., 17° 46' 30" S. 149° 10' 21" W. alt. 50m. 19-vii-80, D.A. & R.E.G. Craig (larvae, CNCI; larvae, MNHP).

Teahupoo, (Tahiti-iti), Tiirahi R., 17° 51' 05" S. 149° 14' 15" W. 20-vii-80, D.A. & R.E.G. Craig (larvae, pupae, BMNH).

Vairoa, (Tahiti-iti), Vavi R., 22-ii-84, P. Schröder (pupa, MNHP).

Mataiea, Vaihiria R., 17° 44' 22" S. 149° 24' 15" W. alt. 80m. 16-vii-80, D.A. & R.E.G. Craig (larvae, DAC); Vaihiria R., 17° 41' 31" S. 149° 25' 02" W. alt. 250m. 17-vii-80, D.A. & R.E.G. Craig (larva, DAC). E. Lac Vaihiria, 17° 40' 58" S. 149° 24' 51" W. alt. 480m. 22-vii-80, D.A. Craig. (pupa, DAC).

Mahaiatea, Taharuu R., 17° 42' 45" S. 149° 29' 15" W. alt. 135m. 15-vii-80, D.A. & R.E.G. Craig (pupae, DSIR).

Paea, Public Gardens, 03-vii-81, D.A. Craig (larvae, DAC).

Punaauia, Punaruu R., 17° 38' 20" S. 149° 35' 05" W. 27-vi-69, B. Hocking (larvae, UASM); 03-v-73 (larvae, pupae, DAC); 05-vii-73 (larvae, UASM), 6-vii-73 (larvae, MNHP), 04-vii-74 (larvae, DAC), 05-vii-74 (larvae, DAC), 08-vii-74 (larvae, DSIR), 18-vii-74 (larvae, CNCI), 07-vii-80 (larvae, DAC), D.A. & R.E.G. Craig.

Simulium (Inseliellum) sp.
(Fig. 17)

Description.—

Adult Female. Unknown.

Adult Male. (Based on pharate material). Head: width 0.6 mm, depth 0.5 mm. Eyes: upper, larger ommatidia 0.04 mm, 12 rows both up and across eye, lower, smaller ommatidia 0.01 mm. Mouthparts: less than 0.50 of head depth; lacinia with hairs apically; palpal sensory vesicle spherical, 0.50 width of article, opening 0.33 width of vesicle, four or five sensillar sockets visible. Legs: segments with pigmented distal regions; pretarsal claw with 17–20 grappling hooks. Genitalia (Fig.17): gonocoxa with pronounced posteromedial projection; gonostylus broad, roundly truncated distally, single prominent apical spine; ventral plate hairy and broadly cone-shaped posteromedially, rounded laterally, anterior arms heavily pigmented, anteromedian notch broad.

Pupa. Thorax: tubercles pointed. Gill: length 1.2 mm; as for *S. oviceps*; dorsal-most filament 0.33 length of other filaments.

Larva. Unknown.

Phylogenetic relationships.— This adult has been placed in the *oviceps*-group on the basis of pupal characteristics, namely the short dorsal gill filament and the pointed thoracic tubercles, both characteristic of *S. oviceps*. However, the genitalia (Fig. 17) with unique large posteromedian projection on the gonocoxa, show that this male is not of *S. oviceps*. Because this specimen may belong to one of the oviceps-group of species that are based only on larvae, it is not given specific status at this time.

Material Examined.— Pupa: pharate adult; as slide mount; label data: Simulium (I.) sp., TAHITI, Mataiea, E. Lac Vaihiria, 17° 40' 58" S. 149° 24' 51" W. alt. 480 m. 22-vii-80, D.A. Craig. Stat. # 16 (MNHP).

CONCLUDING REMARKS

I estimate that only 75% of simuliid species in Tahiti have been described, based on the rate at which species were discovered once it was realized that the new species were from specialized habitats; which had not been well collected. Further, morphological variation indicates that species such as *S. oviceps* and perhaps *S. neoviceps* are probably complexes of species.

When description of the Marquesas (Sechan *in* Klein *et al.*, 1983) and Huahine (Sechan pers. comm.) simuliids are complete, preferably with karyological data, it should be possible to attempt a cladistic analysis for *Inseliellum*. This could be particularly valuable, because it would include almost a total fauna which, to judge from the ages of the islands involved (Duncan and McDougall, 1974; 1976), and from karyological and morphological data, is monophyletic. If so, it should then prove possible to test the zoogeographic hypotheses of Craig (1983) and to make predictions regarding discovery of simuliids on other Polynesian islands.

Such an analysis will require establishing the sister taxon to *Inseliellum* for outgroup comparison. That may prove difficult because of the homogeneous morphological nature of possible candidate subgenera.

Bionomically, Polynesian simuliids are poorly known, but Schröder (1985) has made a valuable start with his studies on feeding behaviour and distribution of Tahitian simuliids. This provides a basis for investigation of resource partitioning by the larvae in relation to their morphological and presumably behavioural characteristics. Of particular interest, but probably very difficult to do, will be examination of the reproductive behaviour which keeps the sympatric species from hybridizing, and the mechanisms by which the very rare species manage to locate mates.

Marquet and Lamarque (1987) report that there are 17 species of fresh water fish in Tahiti and Moorea, and that waterfalls have a marked effect on their distribution. In the larger rivers on Tahiti fish are very common and noticeable (pers. obs.). Fish are known predators of black fly larvae and these can be an important food item (Davies, 1981; Allen, 1982). Further, there are suggestions (Peckarsky, 1984) that such prey organisms may form large groups to reduce chances of predation per individual.

At the Cascades de Faarumai, in particular at the Haamaremarerahi cascade, where the wet rocks directly entered the pool at the base of the cascade, small gobiid sucker-fish (*Sicyopterus taeniurus*) were common on the rock faces. These fish could move with startling agility up and across the wet rock. Upon disturbance, the fish would either swim rapidly up the rock, or leap off into the pool below. Noticeable was that in these situations the rock was bare. Where there was a rubble base to the rock face and the fish did not have direct access to a pool beneath, they did not occur and algae and macrophytes grew in the water flowing over the rock. Black fly larvae were found on the vegetation and patches of bare rock. A search of the bare rock faces above the pool failed to reveal larvae of *S. neoviceps* or, indeed, of any black fly. However, analysis of gut contents of six of the gobiids produced five larval carcasses of the short labral fan-form of *S. oviceps*. The remainder of the gut contents was algae, of which a high proportion was diatomaceous, and small pieces of volcanic glass. The gobiids are apparently browsers, ingesting the black fly larvae incidentally along with the epilithic algae. This observation, in addition to those on distribution of *S. tahitiense* and *S. oviceps* larvae in the larger rivers, where larvae respectively, either form large aggregations, or are in depression in the rocks, suggests that fish feeding behaviour has an effect on distribution of Tahitian Simuliidae. This hypothesis could perhaps be tested by examining the distribution and aggregation behaviour of larvae of black flies species above and below waterfalls high enough to effect distribution of fish.

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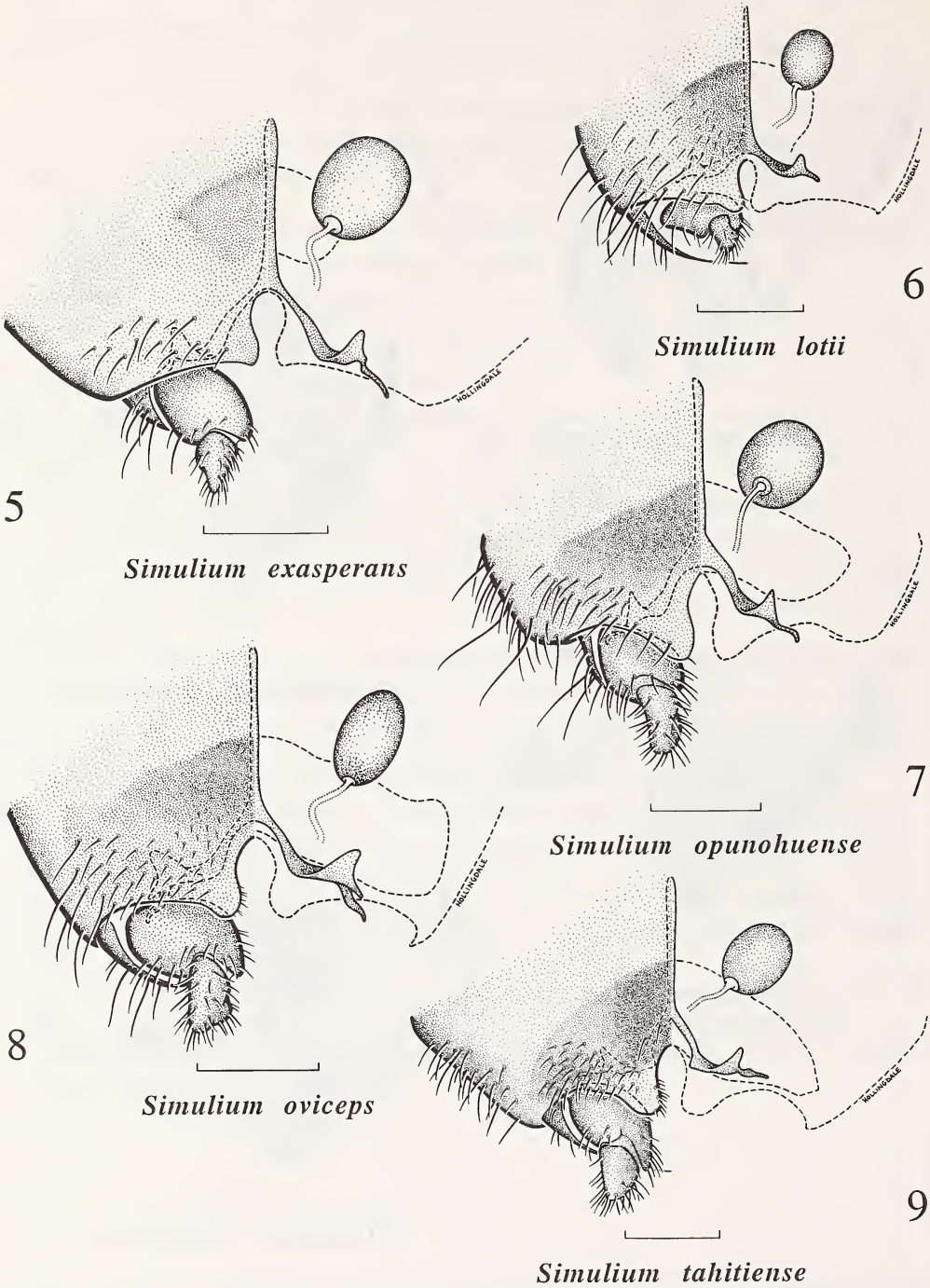
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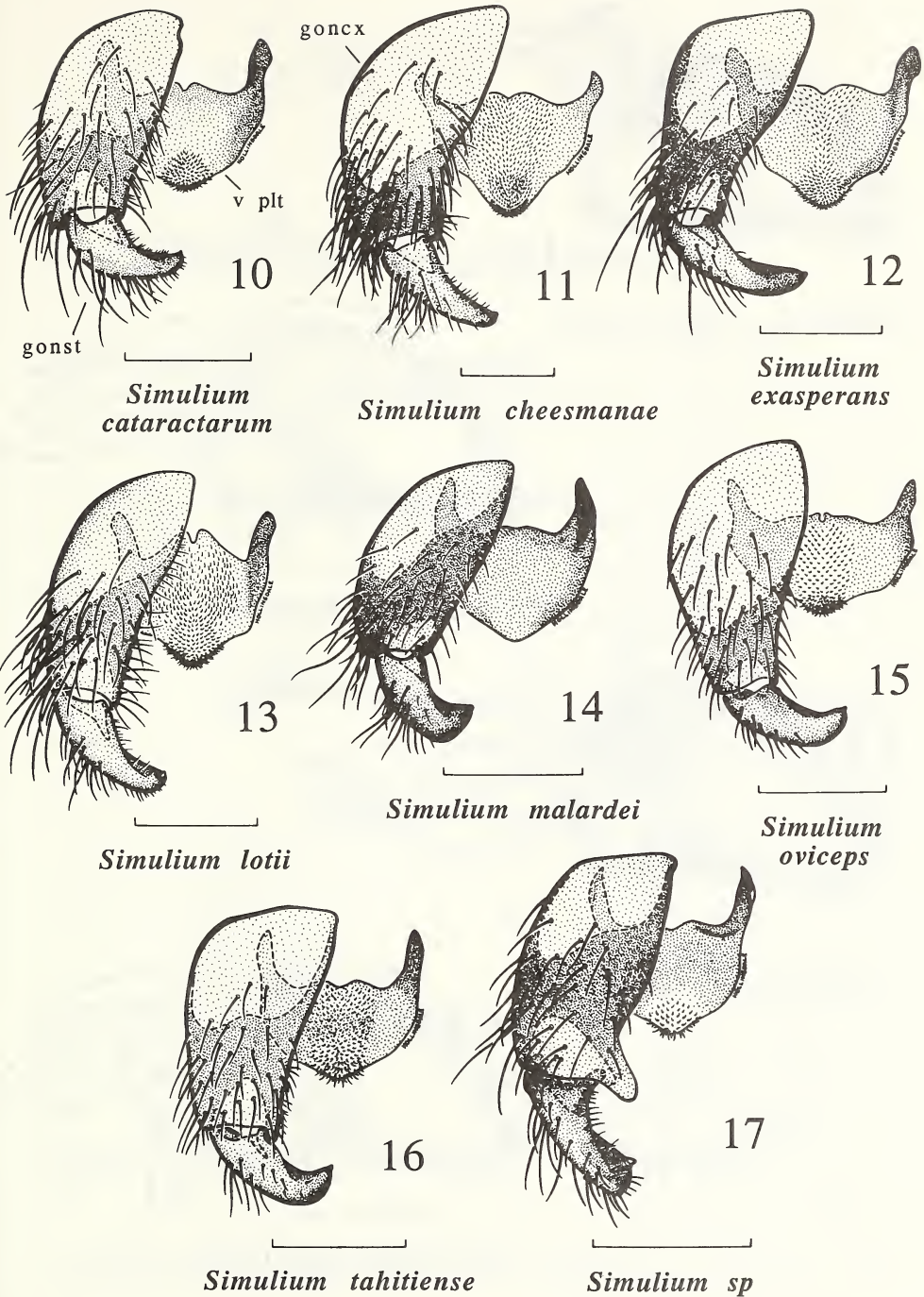
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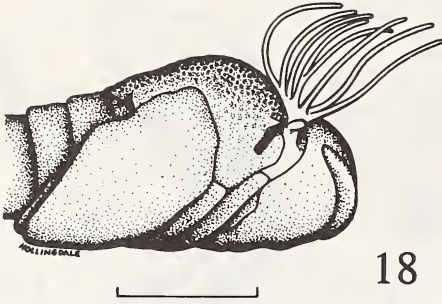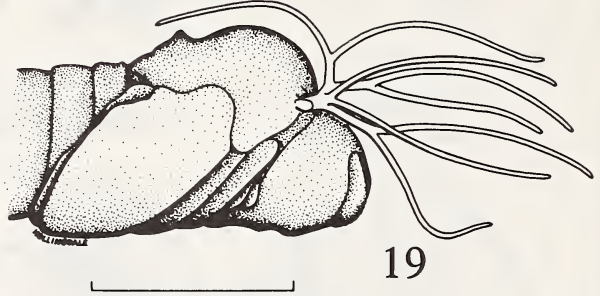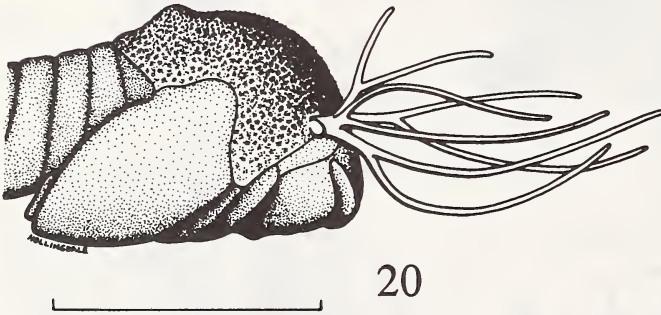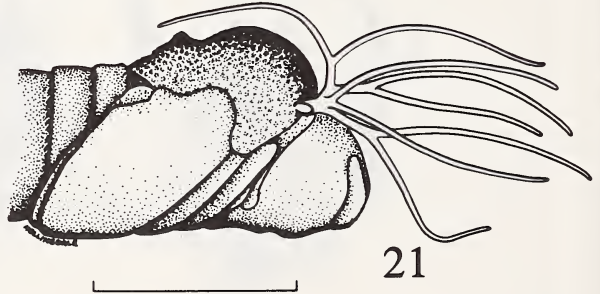
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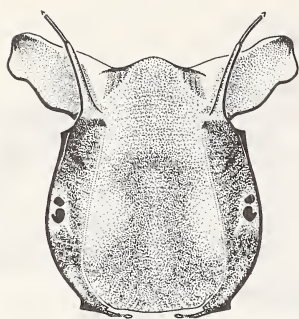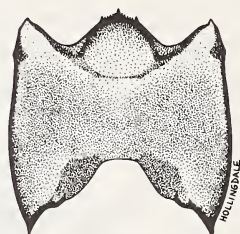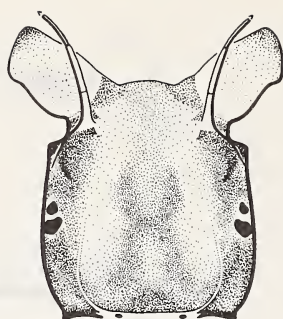
Simulium admixtum   **Simulium arlecchinum**
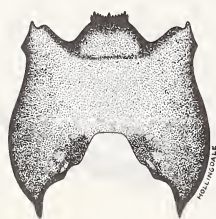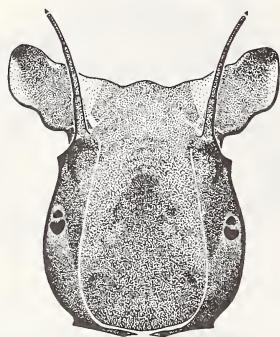
Simulium castaneum   **Simulium cataractarum**

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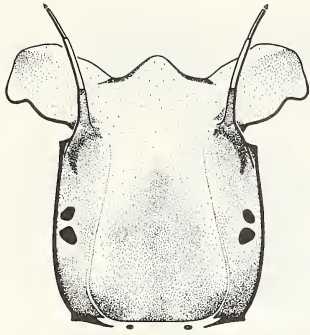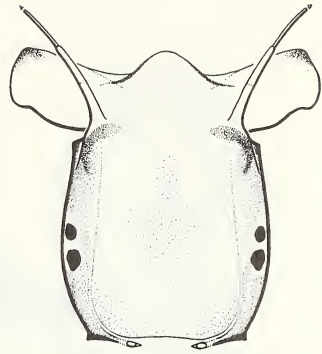
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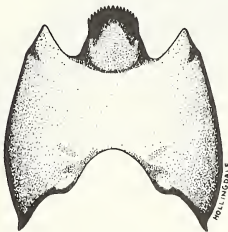
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Simulium neoviceps
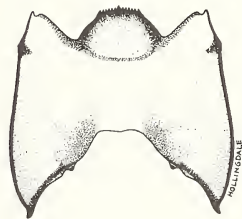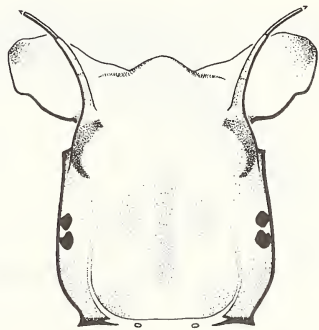
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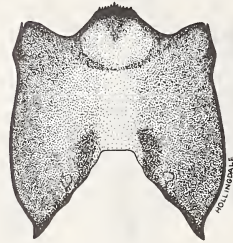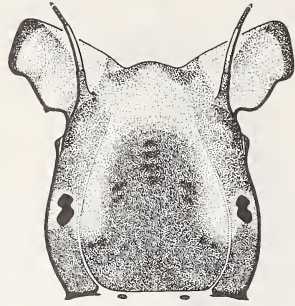
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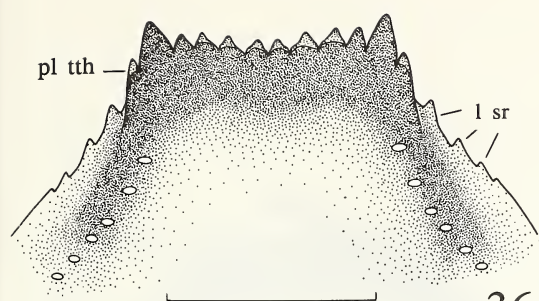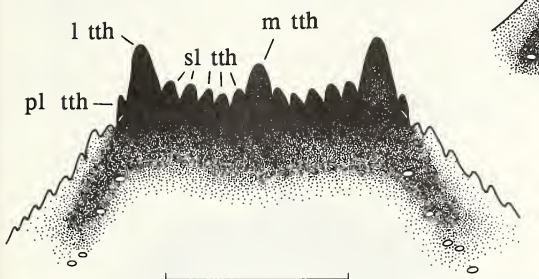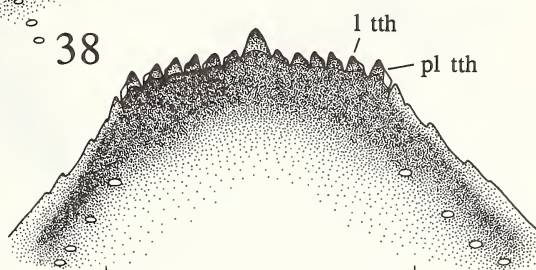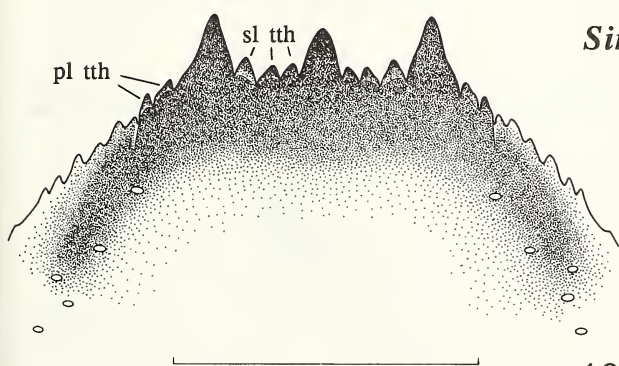
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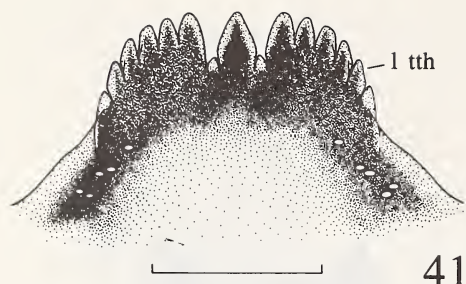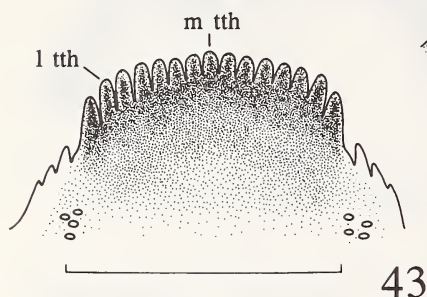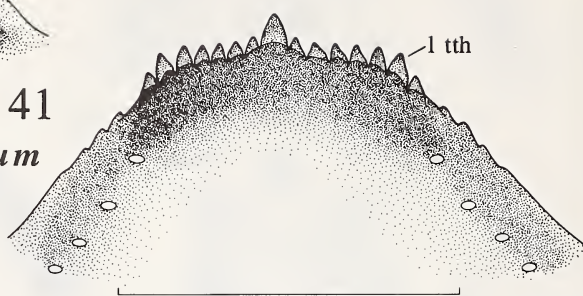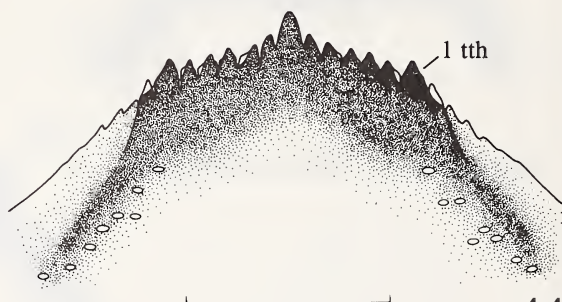
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45 sp tth
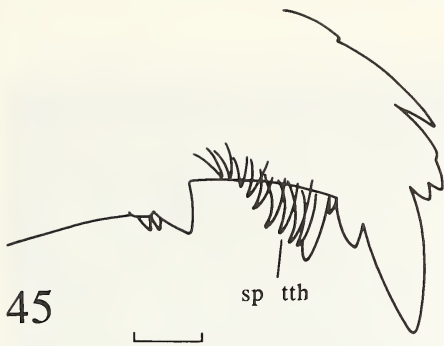
Simulium admixtum

46 s mnd s
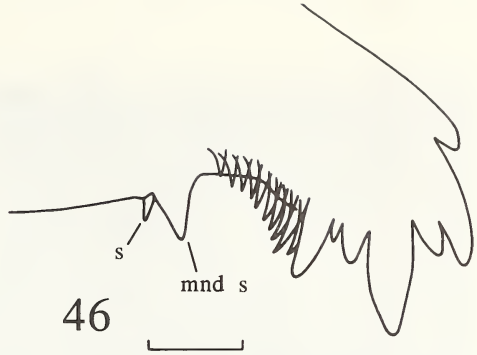
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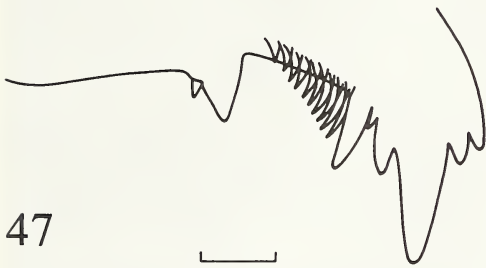
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Simulium castaneum

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Simulium cataractarum

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Simulium exasperans
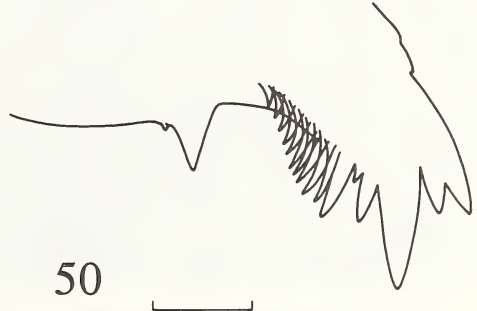
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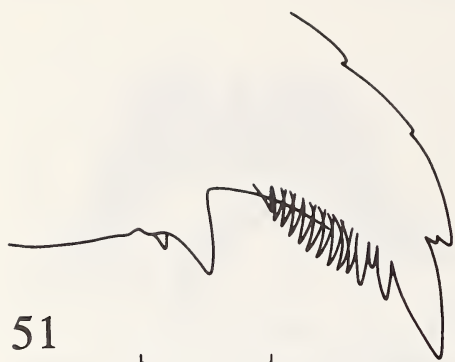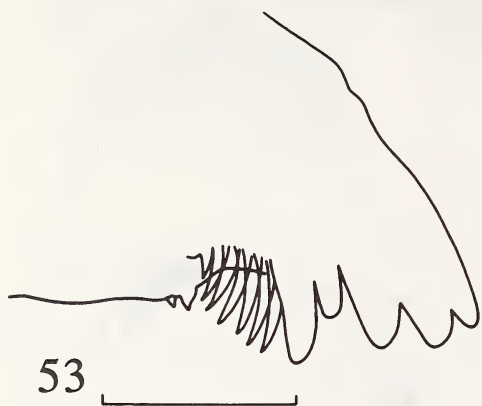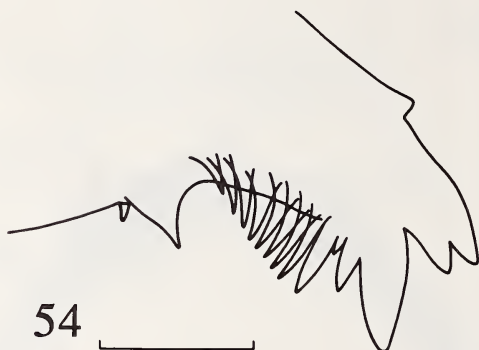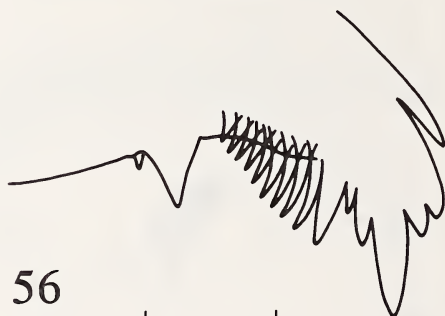
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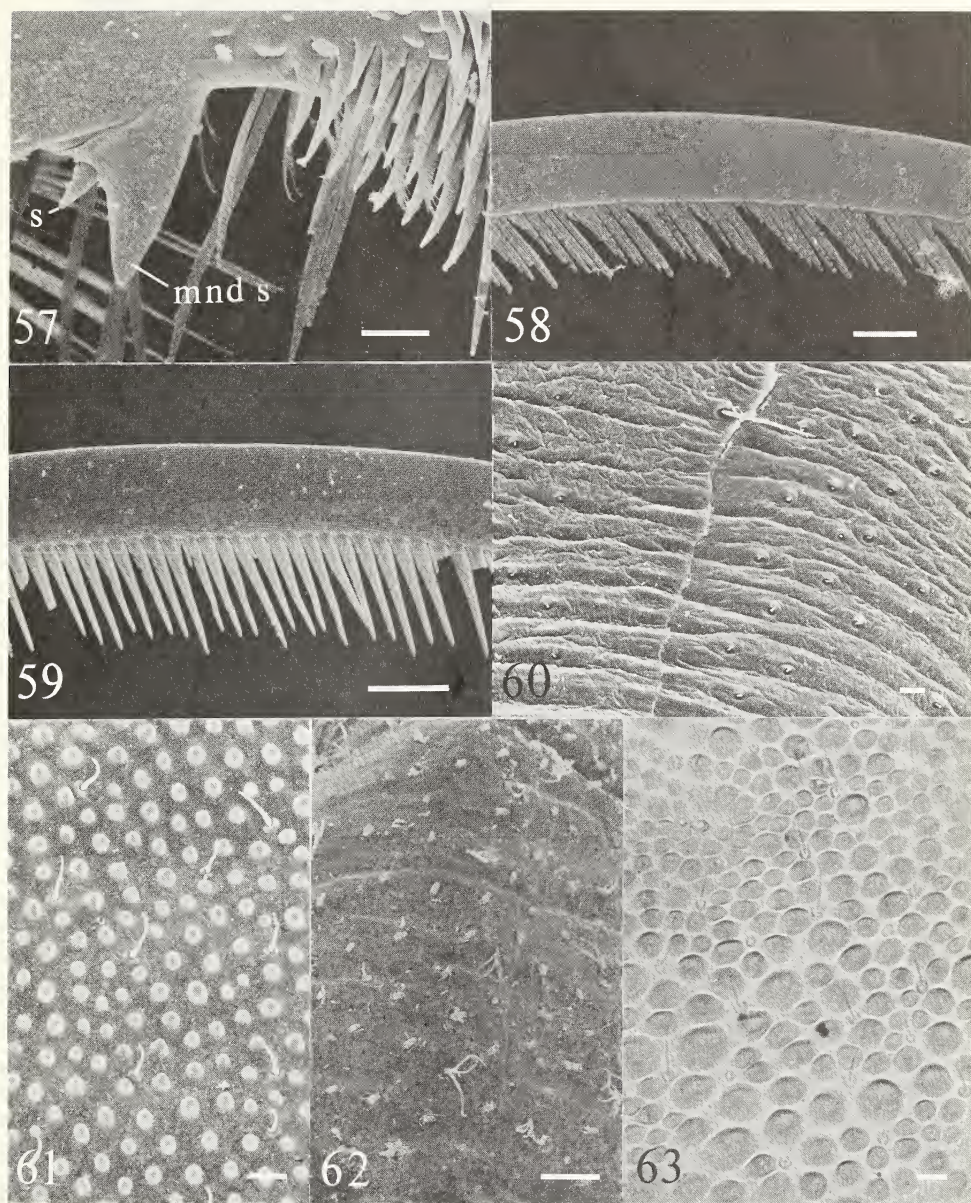
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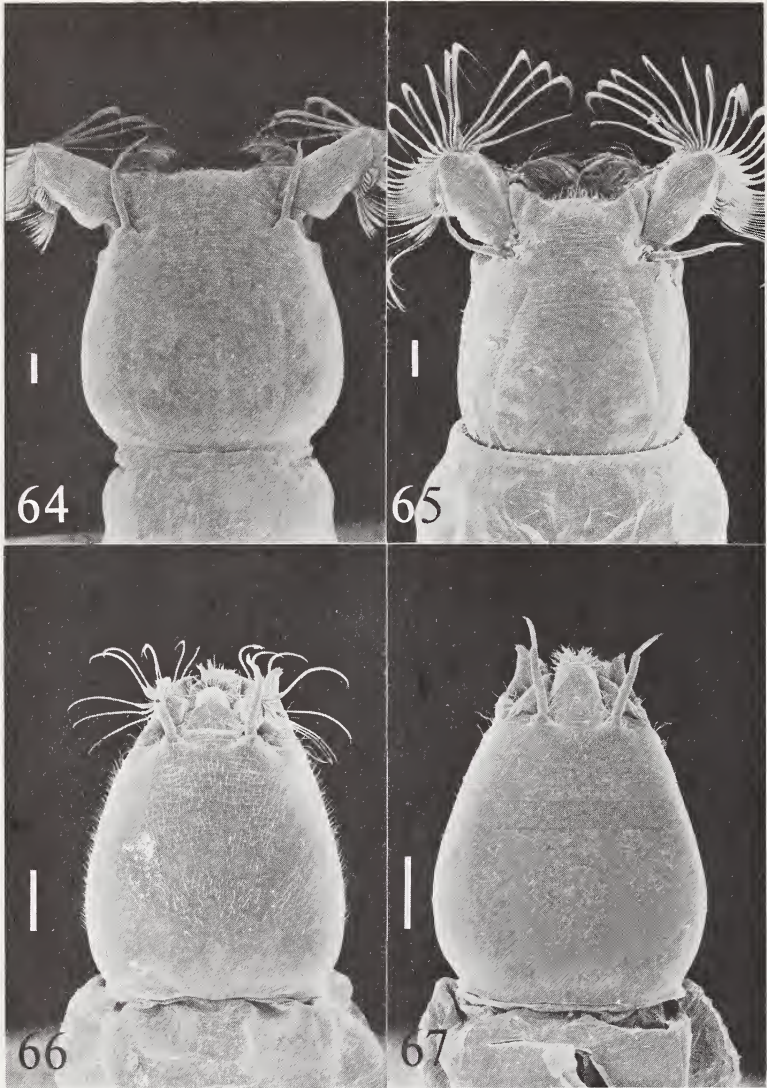
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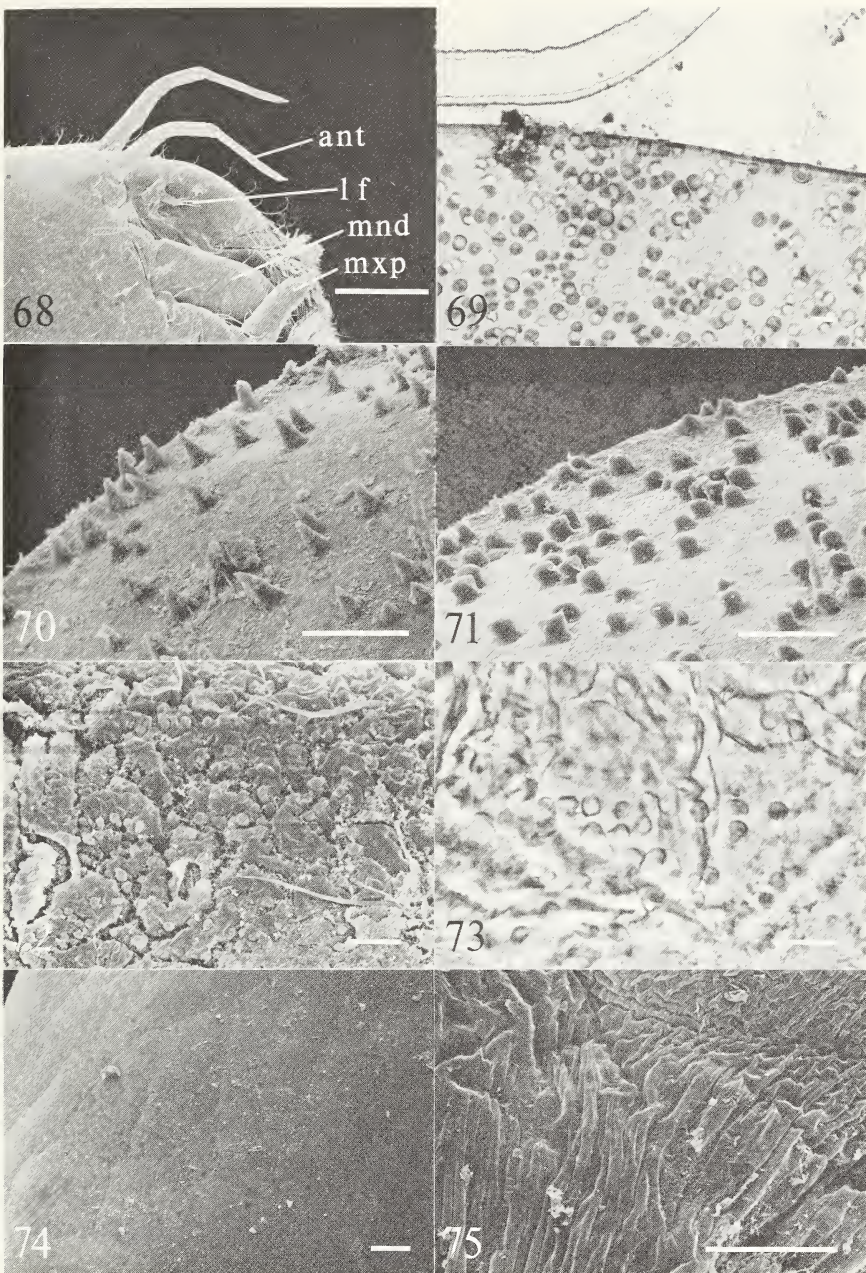
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Entomologicae

A periodical record of entomological investigations,
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SYSTEMATICS, PHYLOGENY AND BIOGEOGRAPHY OF NEW WORLD WEEVILS TRADITIONALLY OF THE TRIBE CLEONINI (COLEOPTERA: CURCULIONIDAE; CLEONINAE)

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ABSTRACT

A survey of representatives of generic-group names in Cleoninae and consideration of their phylogenetic relationships indicates four genera are represented in the New World. These are: Cleonis *Dejean (introduced; 1 species);* Stephanocleonus *Motschulsky (Holarctic, northern; 6 species including* S. confusus *n. sp. [type locality, Black Hills, South Dakota],* S. immaculatus *n. sp. [type locality, Fort McMurray, Alberta],* S. parshus *n. sp. [type locality, Chalk River, Ontario], and* S. stenothorax *n. sp. [type locality, Bluefish Caves, Yukon Territory]);* Apleurus *Chevrolat (southwestern North America, arid lands; 8 species); and,* Cleonidius *Casey (eastern and western North America, semi-arid and arid lands; 19 species including* C. eustictorrhinus *n.sp. [type locality, Sacramento, California],* C. infrequens *n. sp. [type locality, Scott City, Kansas], and,* C. notolomus *n. sp. [type locality, Grant County, New Mexico]).* Cleonidius *is hypothesized to be phylogenetically more closely related to traditional Lixini rather than Cleonini and present tribal classification of Cleoninae is regarded as unsatisfactory. The following new generic-group synonymies are presented:* Lixus *Fabricius (=*Epimeces *Billberg [type species* Curculio filiformis *Fabricius, here designated]);* Stephanocleonus *Motschulsky (=*Coniocleonus *Motschulsky);* Apleurus *Chevrolat (=*Centrocleonus *LeConte,* Cleonopsis *LeConte,* Cleonaspis *LeConte, and* Dinocleus *Casey); and,* Cleonidius *Casey (=*Lixestus *Reitter).*

The following information is given in detail for each of Cleonis, Stephanocleonus, Apleurus (Gibbostethus) *n. subg. (type species,* Dinocleus hystrix *Fall by monotypy),* Apleurus (Apleurus), *and* Cleonidius: *synonymic list, notes about synonymy, diagnosis, description, list of included species, and a discussion of phylogenetic relationships. Keys to species of North American* Stephanocleonus *and* Apleurus, *and world* Cleonidius, *are presented. The following information is given in detail for each species considered: synonymic list, notes about synonymy, problems in recognition, description, distribution, natural history information, and chorological relationships.*

Lixus mixtus *LeConte is a junior homonym and is replaced with* Cleonidius longinasus, *new name. The following new species-group synonymies are presented:* Apleurus lutulentus *(LeConte) (=*Cleonus pulvereus *LeConte,* Apleurus fossus *Chevrolat, and* Dinocleus bryanti *Van Dyke);* Apleurus porosus *(LeConte)(=*Dinocleus farctus *Casey);* Apleurus angularis *(LeConte) (=*Dinocleus denticollis *Casey and* Dinocleus porcatus *Casey);* Apleurus jacobinus *(Casey) (=*Centrocleonus pilosus *LeConte and* Cleonus (Dinocleus) capillosus *Csiki);* Apleurus

albovestitus *(Casey)* *(*=Cleonus molitor *LeConte*, Dinocleus densus *Casey*, Dinocleus wickhami *Casey*, Dinocleus interruptus *Casey*, Dinocleus mexicanus *Casey, and* Cleonus (Dinocleus) structor *Csiki);* Apleurus saginatus *(Casey)* *(*=Dinocleus dentatus *Champion);* Cleonidius subcylindricus *Casey* *(*=Cleonus (Cleonidius) graniferus *Casey);* Cleonidius texanus *(LeConte)* *(*=Cleonus (Cleonidius) circumductus *Casey);* Cleonidius frontalis *(LeConte)* *(*=Cleonus sparsus *LeConte and* Cleonus (Cleonidius) stratus *Csiki);* Cleonidius poricollis *(Mannerheim)* *(*=Cleonus (Cleonidius) lobigerinus *Casey and* Cleonus (Cleonidius) kirbyi *Casey);* Cleonidius boucardi *(Chevrolat)* *(*=Cleonus carinicollis *LeConte and* Cleonus (Cleonidius) lecontellus *Csiki); and,* Cleonidius trivittatus *(Say)* *(*=Cleonus inornatus *LeConte and* Cleonus (Cleonidius) bicarinatus *Casey).* Lixus californicus *Motschulsky is considered a nomen dubium.*

Only for species of Apleurus *and* Cleonidius *are reconstructed phylogenies presented based on analyses of 31 characters in* Apleurus *and 22 characters in* Cleonidius. Apleurus *is hypothesized to be the monophyletic sister genus of the Palearctic* Chromoderus. *In* Apleurus, *two monophyletic subgenera are recognized. These are* Gibbostethus *(1 species,* A. hystrix*) and* Apleurus *s. s. (7 species). Within* Apleurus *s. s. included species and hypothesized phylogenetic relationships are as follows: ((((A.* albovestitus *+ A.* saginatus*) + ((A.* jacobinus *+ A.* angularis*) + A.* porosus*)) + A.* lutulentus*) + A.* aztecus*).* Cleonidius *is monophyletic and hypothesized to comprise an unresolved trichotomy with the Palearctic* Lixus (Lixoglyptus) *and* Cylindropterus. *Four monophyletic species groups are recognized in* Cleonidius. *Along with constituent species and hypothesized phylogenetic relationships, these are:* C. erysimi *group, (((C.* texanus *+ C.* longinasus*) + C.* subcylindricus*) + C.* pleuralis *+ (C.* erysimi *+ C.* eustictorrhinus*));* C. americanus *group, ((((C.* puberulus *+ C.* infrequens*) + (C.* collaris *+ C.* notolomus*)) + C.* canescens*) +(C.* americanus *+ C.* frontalis*));* C. poricollis *group, (C.* poricollis *+ C.* calandroides*); and* C. boucardi *group, (((C.* placidus *+ C.* quadrilineatus*) + C.* trivittatus*) + C.* boucardi*). Phylogenetic relationships of groups are (((C.* boucardi *group +* C. poricollis *group) + C.* americanus *group) + C.* erysimi *group). Phylogenetic relationships of the Nearctic species component of* Cleonidius *are unresolved but the latter is likely sister to the Palearctic species component.*

Both Apleurus *and* Cleonidius *are hypothesized to have entered North America in savanna or grassland habitats (or their precursors) across Beringia during late Eocene time. In North America, primary diversification has taken place in the arid lands of the southwestern United States although two species of* Cleonidius *are found in coastal regions of eastern North America. In both genera there appears to be an initial vicariance of lineages, on Compositae, in grassland or mesquite-grassland habitats between California, central México, and the southern Rocky Mountains. Further speciation events in* Apleurus *appear due primarily to shifts to new, apotypic habitat types at differing altitudes brought about by increased aridity during the later Tertiary; host plant shifts are not a factor because* Apleurus *species are all associated with Compositae. Host plant shifts, however, primarily between Leguminosae-Rosaceae and likely also Compositae-Cruciferae, and within-habitat-type allopatric speciation appear to predominate as the causes of further speciation in* Cleonidius, *most species of which remain associated with plesiotypic less-arid habitat types. Habitat shifts promoting speciation in* Cleonidius *are evident, but are not as associated with formation of increasingly arid habitats as in* Apleurus.

Evolutionary trends in Apleurus *and* Cleonidius *are discussed and patterns and predictions of biogeographic or evolutionary interest summarized and presented for examination for*

general applicability.

RÉSUMÉ

Une diagnose des charactres de la sous-famille est aussi brièvement discutée. L'examen de représentants des groupes-genres de Cleoninae et leurs relations phylétiques indiquent que quatre genres sont représentés dans le Nouveau-Monde. Ils sont: Cleonis *Dejean (introduit; 1 espèce);* Stephanocleonus *Motschulsky (Holoartique, nordique; 6 espèces incluant S. confusus n. esp [localité-type, Black Hills, Dakota du Sud], S. immaculatus n. esp [localité-type, Fort McMurray, Alberta], S. parshus n. esp [localité-type, Chalk River, Ontario], et S. stenothorax n. esp [localité-type, Bluefish Caves, Territoire du Yukon];* Apleurus *Chevrolat (sud-ouest de l'Amérique du Nord, terres arides; 8 espèces); et* Cleonidius *Casey (est et ouest de l'Amérique du Nord, terres arides et semi-arides; 19 espèces incluant C. eustictorrhinus n. esp [localité-type, Sacramento, Califournie], C. infrequens n. esp. [localité-type, Scott City, Kansas], et C. notolomus n. esp. [localité-type, Grant County, Nouveau Mexique].* Cleonidius *est suggéré comme étant phylétiquement plus apparenté aux traditionels Lixini plutôt qu'aux Cleonini, et la classification actuelle de Cleoninae est considérée comme étant insatisfaisante. De nouvelles synonymies de groupe-genres sont présentée:* Lixus *Fabricius (=Epimeces Billberg [espèce-type Curculio filiformis Fabricius, ici désignée]);* Stephanocleonus *Motschulsky (=Coniocleonus Motschulsky);* Apleurus *Chevrolat (=Centrocleonus LeConte, Cleonopsis LeConte, Cleonaspis LeConte, et Dinocleus Casey); et* Cleonidius *Casey (=Lixestus Reitter).*

L'information suivante est présentée en détail pour chacun des Cleonis, Stephanocleonus, Apleurus *(Gibbostethus) nouveau sous-genre,* Dinocleus hystrix *Fall par monotypie),* Apleurus *(Apleurus), et* Cleonidius: *liste synonymique et notes les concernant, diagnose, description, liste des espèces incluses, et une discussion concernant les relations phylétiques. Des clefs d'identification à l'espèce pour les* Stephanocleonus *et* Apleurus *de l'Amérique du Nord, et les* Cleonidius *Mondiaux sont produites. L'information suivante est aussi présentée en détail pour chacune des espèces considérées: liste synonymique et notes les concernant, problèmes associés à l'identification, description, distribution, histoire naturelle, et relations chorologiques.*

Lixus mixtus *LeConte est considéré comme homonyme plus récent et est remplacé par* Cleonidius longinasus, *nouveau nom. Les nouvelles synonymies suivantes des groupes-espèces sont présentées:* Apleurus lutulentus *(LeConte), (=Cleonis pulvereus LeConte,* Apleurus fossus *Chevrolat, et* Dinocleus bryanti *Van Dyke);* Apleurus porosus *(LeConte) (=Dinocleus farctus Casey);* Apleurus angularis *(LeConte) (=Dinocleus denticollis Casey et Dinocleus porcatus Casey);* Apleurus jacobinus *(Casey) (=Centrocleonus pilosus LeConte et Cleonus (Dinocleus) capillosus Csiki);* Apleurus albovestitus *(Casey) (=Cleonus molitor LeConte, Dinocleus densus Casey, Dinocleus wickhami Casey, Dinocleus interruptus Casey, Dinocleus mexicanus Casey, et Cleonus (Dinocleus) structor Csiki);* Apleurus saginatus *(Casey) (=Dinocleus dentatus Champion);* Cleonidius subcylindricus *Casey (=Cleonus (Cleonidius) graniferus Casey);* Cleonidius texanus *(LeConte) (=Cleonus (Cleonidius) circumductus Casey);* Cleonidius frontalis *(LeConte) (=Cleonus sparsus LeConte et Cleonus (Cleonidius) stratus Csiki);* Cleonidius poricollis *(Mannerheim) (=Cleonus (Cleonidius) lobigerinus Casey et Cleonus (Cleonidius) kirbyi Casey);* Cleonidius boucardi *(Chevrolat) (=Cleonus carinicollis LeConte et Cleonus (Cleonidius) lecontellus Csiki); et* Cleonidius trivittatus *(Say) (=Cleonus inornatus LeConte et Cleonus (Cleonidius) bicarinatus Casey).* Lixus californicus *Motschulsky est considérée nomen dubium.*

*Des reconstitutions phylétiques sont présentées pour les espèces d'*Apleurus *et* Cleonidius *uniquement, et sont basées sur l'analyse de 31 charactères pour* Apleurus *et 22 charactères pour* Cleonidius. Apleurus *est suggéré comme étant le genre-soeur monophylétique du* Chromoderus *paléartique. À l'intérieur d'*Alleurus, *deux sous-genres monophylétiques sont reconnus. Ils sont* Gibbostethus *(1 espèce, A. hystrix) et* Apleurus s. s. *(7 espèces). À l'intérieur d'*Apleurus s. s. *les espèces incluses ainsi que les relations phylétiques suggérées sont les suivantes: ((((A. albovestitus + A. saginatus + ((A. jacobinus + A. angularis) + A. porosus)) + A. lutulentus) + A. aztecus).* Cleonidius *est monophylétique et est proposé comme englobant une trichotomie non-résolue avec le* Lixus *(Lixoglyptus) paléartique et* Cylindropterus. *Quatre groupe-espèces monophylétiques sont reconnus pour* Cleonidius. *De conserve avec les espèces constituantes et les relations phylétiques suggérées, ils sont: le groupe C. erysimi, (((C. texanus + C. longinasus) + C. subcylindricus) + C. pleuralis + (C. erysimi + C. eustictorrhinus)); le groupe C. americanus, ((((C. puberulus + C. infrequens) + (C. collaris + C. notolomus)) + C. canescens) + C. americanus + C. frontalis)); le groupe C. poricollis, (C. poricollis + C. calandroides); et le groupe C. boucardi, (((C. placidus + C. quadrilineatus) + C. trivattatus) + C. boucardi). Les relations phylétiques des groupes sont: (((C. boucardi groupe + C. poricollis groupe + C. americanus groupe + C. erysimi groupe. Les relations phylétiques entre les espèces de* Cleonidius *de la composante néartique sont non-résolues, cependent cette dernière est vraisemblablement soeur de la composante paléartique.*

*L'hypothèse qu'*Apleurus *et* Cleonidius *atteignirent l'Amérique du Nord via Béringia, aux travers des savanes ou des prairies (ou de leurs précurseurs) durant l'Éocène supérieur, est avancée. En Amérique du Nord, une diversification initiale aurait pris place dans les terres arides du sud-ouest des États-Unis, bien que deux espèces de* Cleonidius *soient retrouvées dans les régions côtières de l'est de l'Amérique du Nord. Il semble, qu'à l'intérieur de ces deux genres, les lignées démontrent une vicariance initiale, sur Compositae, en prairies avec ou sans mesquites entre la Califournie, le Mexique Central, et le sud des Montagnes Rocheuses. Plus ample évènements de spéciation chez* Apleurus *sont apparus dûes principalement aux déplacements vers de nouveaux habitats apotypiques-types aux différantes altitudes, induits par l'aridité accrue raignant au Tertiaire supérieur; le déplacement vers de nouvelles plantes-hôtes n'est pas un facteur*

*puisque toutes les espèces d'*Apleurus *sont associées aux* Compositae. *Cependent, le déplacement vers de nouvelles plantes-hôtes, principalement entre* Leguminosae-Rosacae *et vraisemblablement* Compositae-Cruciferae, *de-même qu'une spéciation intra-habitats de type allopatrique semblent dominer en tant qu'instigateurs de plus ample spéciations chez* Cleonidius, *la majorité de ces dernier demeurant associés à la formation d'habitats plésiotypiques moins arides. Les déplacement vers de nouveaux habitats encourageant la spéciation chez* Cleonidius *sont évidents, mais ne sont pas aussi fortement associés à l'apparition d'habitats de plus en plus arides comme chez* Apleurus.*

Les tendances évolutionaires chez Apleurus *et* Cleonidius *sont discutées et les patrons de distribution ainsi que des prédictions d'intérèts biogéographiques ou évolutionaires sont résumés et présentés pour examen de leur applicabilité globale.*

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INTRODUCTION

J.B.S. Haldane, in an oft repeated quote, once stated that the creator must have held a special fondness for beetles for he made so many of them. To this I would hasten to add that he must also have had a special predilection towards weevils, for the Curculionidae are the largest single family of organisms known. More than 44883 species had been described as of 1971 (O'Brien and Wibmer, 1978) and countless others no doubt await discovery and formal scientific description. In so far as numerous species await description, some clearer understanding has yet to be achieved of those taxa already formally recognized. Crowson (1955), commenting on this very problem, noted that "A satisfactory resolution of the Curculionidae into subfamilies and tribes is probably the largest and most important

outstanding problem in the higher classification of Coleoptera particularly as a great number of the species are more or less seriously injurious to economically valuable crops."

But to begin to make progress towards achieving this goal, we must start at some lower level, come to some understanding of a subfamily, tribe or genus, and then proceed to the larger and more complex problem. This I have chosen to do by conducting a study of the North American species that have traditionally been placed in the tribe Cleonini of the Cleoninae. The group had not been revised since LeConte and Horn (1876) and subsequently Casey (1891), and has been recently widely recognized by curculionid systematists as problematical and in need of work. Not only were species very difficult to reliably identify, but classification of the North American fauna in a world perspective had not been attempted. Use of the group in applied problems (*e.g.,* as biological control agents of pest weeds), or to address theoretical problems of general evolutionary or biogeographic importance, was not yet possible.

This study will alleviate those problems of identification and provide more detailed and reliable definitions of species and species-group taxa than those previously presented. It will also address the classification of the North American fauna in a world perspective and represent a start at a consistent scheme for use by scientists in all faunal regions. Phylogenetic and biogeographic patterns can then be recognized and resultant process-hypotheses formulated so as to be available for general consideration and applicability by students from a wide array of disciplines, not just those interested in Curculionoidea.

MATERIALS AND METHODS

Materials

This study was based on examination of 9498 adult specimens of *Cleonidius* (3586); *Apleurus* (5627); North American *Stephanocleonus* (224), and *Cleonis pigra* (61), borrowed from various collections, both institutional and private, and including material I personally collected in the western United States and Canada. The following codens represent these collections, both individual and institutional, and their respective curators.

AMNH   American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024, U.S.A.; L.H. Herman.

ASUT   Arizona State University, Tempe, Arizona, 85281, U.S.A.; F.F. Hasbrouck.

BMNH   British Museum (Natural History), Cromwell Road, London, SW7 5BD, England; R.T. Thompson and C.H.C. Lyal.

CASC   California Academy of Sciences, Department of Entomology, Golden Gate Park, San Francisco, California, 94118, U.S.A.; D.H. Kavanaugh.

CDFA   California Department of Food and Agriculture, 1220 N Street, Sacramento, California, 95814, U.S.A.; T.N. Seeno.

CNCI   Canadian National Collection of Insects, Arachnids and Nematodes, Biosystematics Research Centre, Research Branch, Ottawa, Ontario, K1A 0C6, Canada; D.E. Bright.

CUIC   Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, New York, 14853, U.S.A.; J.K. Liebherr.

CWOB   Charles W. O'Brien Collection, Department of Entomology, Florida Agricultural and Mechanical University, Tallahassee, Florida, 32307, U.S.A.; C.W. O'Brien.

DLCC   Douglas L. Caldwell Collection, Chemical Lawn R & D Center, P.O. Box 395, Milford Center, Ohio, 43045, U.S.A.; D.L. Caldwell.

ELSC   Elbert L. Sleeper Collection, Department of Biology, California State University at Long Beach, Long Beach, California, 90801, U.S.A.; E.L. Sleeper.

FMNH   Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois, 60605, U.S.A.; L.E. Watrous.

HAHC   Henry F. and Anne T. Howden Collection, Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6, Canada; A.T. Howden.

JLCC   John L. and Alberta F. Carr Collection, 23 Dalrymple Green NW, Calgary, Alberta, T3A 1Y2, Canada; J.L. Carr.

JVMC   John V. Matthews Collection, Energy, Mines, and Resources Canada, 601 Booth Street, Ottawa, Ontario, K1A 0E8, Canada; J.V. Matthews.

LACM   Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California, 90007, U.S.A.; R.R. Snelling.

MCZC   Museum of Comparative Zoology, Harvard University, Cambridge, MAssachusetts, 02138, U.S.A.; A.F. Newton, Jr.

MNHP   Muséum National d'Histoire Naturelle, Entomologie, 45 Rue Buffon, Paris, France; N. Berti.

MSUC   Montana State University, Department of Biology , Bozeman, Montana, 59717, U.S.A.; S. Rose.

NMSU   New Mexico State University, Department of Biology, Las Cruces, New Mexico, 88003, U.S.A.; J.R. Zimmerman.

NRS   Naturhistoriska Riksmuseet, Sektionen för entomologi, S-104 05, Stockholm, Sweden; P.I. Persson.

NSDA   Nevada State Department of Agriculture, 350 Capitol Hill Avenue, P.O. Box 11100, Reno, Nevada, 89510, U.S.A.; R.C. Bechtel.

OSDA   Oregon State Department of Agriculture, 635 Capitol Street N.E., Salem, Oregon, 97310, U.S.A.; R.L. Westcott.

OSUC   Oregon State University, Department of Entomology, Corvallis, Oregon, 97331, U.S.A.; G.L. Peters.

PUL   Purdue University, Department of Entomology, West Lafayette, Indiana, 47907, U.S.A.; A. Provonsha.

RSAN   denotes specimens in my own personal collection.

SBMN   Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California, 93105, U.S.A.; S. Miller and L. Marx.

SMC   Scott McCleve Collection, 2210 13th Street, Douglas, Arizona, 85607, U.S.A.; S. McCleve.

TAMU   Texas Agricultural and Mechanical University, Department of Entomology, College Station, Texas, 77843, U.S.A.; H.R. Burke.

UASM   University of Alberta, Strickland Museum, Department of Entomology, Edmonton, Alberta, T6G 2E3, Canada; G.E. Ball and D. Shpeley.

UAT   University of Arizona, Department of Entomology, Tucson, Arizona, 85721, U.S.A.; F.G. Werner.

UCBC   University of California, Division of Entomology and Parasitology, Berkeley, California, 94720, U.S.A.; J.A. Chemsak.

UCMC   University of Colorado Museum, Campus Box 218, Boulder, Colorado;
        U.N. Lanham.
UIM   University of Idaho, Department of Entomology, Moscow, Idaho, 83843,
        U.S.A.; W.F. Barr.
UNSM   University of Nebraska State Museum, Research and Systematics
        Collections, W-436 Nebraska Hall, Lincoln, Nebraska, 68588, U.S.A.;
        B.C. Ratcliffe.
USNM   United States National Museum (Natural History), Washington D.C.,
        20560, U.S.A.; D.R. Whitehead.
WECC   Wayne E. Clark Collection, Department of Entomology, Auburn
        University, Auburn, Alabama, 36849, U.S.A.; W.E. Clark.
WSU   Washington State University, Department of Entomology, Pullman,
        Washington, 99164, U.S.A.; R.S. Zack.
ZMMU   Zoological Museum of the Moscow Lomonosov State University, Herzen
        Street 6, Moscow K-9, U.S.S.R.; N. Nikitsky.

Classification of the North American fauna in a world perspective required knowledge of structural diversity of taxa from other regions of the world. In view of this, representatives of type-species (where designated) of 50 of a total of 77 described genus-group names of the tribe Cleonini (not including New World taxa or junior homonyms where replacement names are available) from the British Museum (Natural History) were studied. In instances where a type-species has not been designated for a given genus-group name, representatives of a species initially placed in that taxon (and thus available for subsequent designation as type-species) were selected for study. These taxa are listed in Appendix II.

Methods

Collection of specimens.— Most specimens of Cleoninae collected by me were acquired simply by placing a standard entomological beating sheet underneath foliage of a particular plant and then striking the plant sharply with a sturdy stick in a downward motion over the sheet. Weevils then on the plant feign death and drop downward onto the white sheet where they are easily seen and captured. Specimens were killed in vials containing fine ethyl acetate-soaked wood chips. A few specimens were also collected by sweeping low vegetation or were handpicked from bare soil. Deciduous shrubs in oak-pinyon-juniper woodlands and annual or perennial woody shrubs along dry stream beds, desert washes, or various lotic waterways were the most productive places to concentrate collecting efforts.

Specimen preparation and examination.— A Wild M5® stereo dissecting microscope was used for routine examination of external structural features of dried adult specimens. Dissections were made of mouthparts and internal genitalia and these were examined with both a Wild M5® dissecting microscope and a Leitz SM-Lux® compound brightfield microscope. Special preparation procedures for specific characters examined in detail are given following. For such characters, note is made in the text of the number of specimens that were examined in detail.

For each species, a variable number of male and female individuals were selected from various localities for study of internal genitalic structure. Individuals of both sexes were first softened by immersion in hot distilled water, to which a few drops of liquid soap had been added. Dissection consisted of insertion of the apices of a pair of fine forceps into the sternal

suture separating the base of the abdomen from the metasternum. Careful application of pressure resulted in separation of the abdomen which was then placed into hot 5–10% KOH (aqueous) for a variable amount of time to remove soft tissues. Repeated examinations were made of the abdomen during this process to determine the suitable degree of treatment. The abdomen was then transferred to a 5–10% acetic acid-alcohol solution to neutralize KOH activity, and then to distilled water. Genitalia were then removed from the abdomen and placed in 95% ethanol and then into glycerine for subsequent examination. The abdomen was dried and mounted on a card placed on the specimen pin.

No special techniques were used in the examination of female genitalia; however, for the internal sac of the aedeagus of males to be adequately examined, it was necessary that it be everted and inflated. This was best accomplished using an unpublished technique devised by Mr. Richard T. Thompson of the British Museum (Natural History).

Most practical for large specimens, this technique consists of eversion of the internal sac following softening and treatment with KOH by careful insertion of a hooked minuten pin mounted on the end of a wooden probe into the apex of the aedeagus. Slow and numerous repeated tugs on the sac, which is visible through the wall of the aedeagus, worked best and could be continued until the sac was completely everted, the apical sclerite complex exposed and apical. Attempts to extract the sac rapidly and using only one or a few insertions of the minuten pin frequently damaged the sac such that inflation was not possible. Following eversion, the aedeagus was placed in a liquid (water was used most frequently but a liquid of higher viscosity, such as glycerine, is recommended). The base of the aedeagus was placed at the end of a narrow piece of flexible rubber tubing and the rubber adjacent to the base of the aedeagus pinched with a pair of flat-tipped forceps placed firmly in a hole in a rubber stopper attached to a sturdy metal stand. A continuous force was maintained on the forceps by placing a small elastic band around the forceps near their apices such that they needed to be forced open using another pair of forceps. It was important that the aedeagus was held firmly in place in the apex of the tubing, but that the base of the aedeagus was not sealed by the forceps. The other end of the piece of tubing was attached to a syringe filled with the liquid in which the aedeagus was immersed. The syringe was also placed in a hole in a rubber stopper attached to a separate sturdy metal stand. Gentle pressure on the syringe forced the liquid out the apex of the tubing but ideally only through the aedeagus and thus the internal sac. As liquid passed into the sac it became inflated and remained so for short periods of time while the pressure exerted by the syringe continued to exceed the force limiting inflation of the sac. Drawings were thus made of the sac by repeated application of slight pressure on the syringe. Various views of the sac were obtained by manipulation of the aedeagus in the apex of the tubing and repetition of entire procedure. Proper placement of the base of the aedeagus in the tubing was often difficult because more often than not, pressure on the syringe did not inflate the sac because either the forceps were sealing the base of the aedeagus or, too much liquid was passing out the tubing adjacent to the base of the aedeagus and not through it. In this latter instance the aedeagus was expelled from the apex of the tubing because it was not held firmly in place by the pressure exerted onto the tubing by the forceps. Repeated attempts and manipulation of the location of pressure of the forceps were required for good results.

Following examination, internal genitalia were placed in glycerine in a microvial attached to the specimen pin. To examine mouthparts, heads were removed from individuals softened as noted above, and placed in 5–10% KOH (aqueous) for a variable amount of time as required for removal of soft tissues. The head was then transferred to a 10% hydrogen peroxide-95%

ethanol solution to bleach cuticle to facilitate examination of surface features with a brightfield microscope. Following removal to a 95% ethanol-distilled water solution, maxillary palpi and the prementum were carefully removed from the head by severing connections to the apex of the rostrum with a hooked minuten pin mounted on a wooden probe. These structures were then transferred to glycerine on a depression slide for detailed examination using a brightfield microscope. The head was air dried and mounted on a card placed on the specimen pin. Following examination, mouthparts were placed in glycerine in a microvial attached to the specimen pin. Detailed mouthpart examination was only carried out for species of *Apleurus*. Initial surveys of diversity of mouthpart structure in *Cleonidius* and *Stephanocleonus* species did not prove promising and were discontinued.

Structural terms.— Structural terms follow those of Kissinger (1970) except as noted in Anderson (1984b). Structure of the internal sac of the aedeagus of males in Cleoninae has not been previously studied and an informal nomenclature has been developed (Fig. 115). Future detailed studies on other Cleoninae should result in a more formal nomenclature based on apparent homology between structures in a more comprehensive survey of structural diversity.

Ambiguity in descriptors used in association with various structural terms is a problem worthy of comment. Objectively delimited character states (*e.g.,* presence/absence, red/black, three setae/one seta, *etc.*) are ideal for taxonomic and phylogenetic purposes because there is no ambiguity in assigning a state to a particular taxon. Most character states however, are subjectively expressed (*e.g.,* elongate-narrow/robust, large/small, deep/shallow, *etc.*). For these latter characters to be maximally useful in a taxonomic sense as criteria for identification or otherwise, ambiguity must be reduced in assigning a state to a particular taxon without requiring reference to other taxa. I have attempted to do this for those character states that are taxonomically important in this study but which are not augmented in the text in a quantitative manner or accompanied with figures. Characters and their states in which there is little ambiguity involved are not considered.

Vestiture. I term all body vestiture of apparent non-sensory primary function as scales. Body vestiture is important both phylogenetically and taxonomically. Pronotal scale patterns serve to distinguish genera, elytral scale patterns species of *Stephanocleonus*, and species groups and species of *Cleonidius*. Abdominal scale patterns are important in separating some species of *Apleurus*.

Scales vary from flat or appressed, to recumbent, sub-erect and erect. I use the terms flat or appressed for scales at an angle of 0°–5° relative to body surface; recumbent, 6°–45°; sub-erect, 46°–85°; and erect, 86°–90°.

Shape and size of the scale is important in determining macroscopic patterns of surface vestiture. Small, fine scales obscure less of the underlying dark cuticle and thus the ground color of the cuticle predominates in the pattern; larger, robust scales obscure more cuticle and impart a predominantly whitish color to the pattern. Density of the scales is not as important as size and shape in determining the macroscopic pattern.

More elongate, sub-erect or erect scales are termed "hair-like scales", a name that would correspond to most concepts of "hair". Length of "hair-like scales" is important both taxonomically and phylogenetically. Members of some species clearly lack sub-erect or erect surface vestiture; members of most species have short sub-erect or erect vestiture that is not more than approximately twice the length of the largest appressed scales on that particular body part. Members of few species have moderately long sub-erect or erect vestiture between twice and three times the length of the largest appressed scale. Finally, members of few species have long vestiture, greater than three times the length of the largest appressed scale. Sub-erect

or erect vestiture is abraded to various degrees on some specimens causing problems in identification.

Density of all vestiture and size of scales are indicated qualitatively with reference to other taxa.

Punctation. Punctation is important both phylogenetically and taxonomically. Three aspects of punctation are described: size, density and depth. States of all three aspects are part of a continuum from small, sparse or shallow, to large, dense and deep.

Density of punctation is defined on the basis of the relationship between diameter of a puncture and the distance between it and adjacent punctures. Sparse punctures are those with diameters less than the distance between punctures; moderately dense are those with diameters more or less equal to the distance between punctures; and dense are those with diameters exceeding the distance between punctures.

Size and depth of punctation are more difficult to assess in an objective manner. Shallow punctures are those with the walls of the puncture at about a 45° angle or less; deep are those with walls between 45° and 90°. Moderately deep are those with the state difficult to assign as either deep or shallow. Small punctures are those where a very rough estimate of the number of punctures, if lined side by side spanning that body part, would number more than 50; large are those where the number is less than 25. Estimates between 25 and 50 are considered moderately large.

Punctation of the head, rostrum and pronotum are most important and most frequently referred to in keys and descriptions.

Illustrations.— With the specimen placed in glycerine, all drawings of genitalia and mouthparts were made on paper with the aid of a camera lucida attached to Wild M5® or Leitz SM-Lux® microscopes at various magnifications and later traced, then inked, onto mylar drafting film for reproduction. Drawings of other structural features were similarly made of dried pinned specimens with the aid of a camera lucida attached to a Wild M5® microscope. Details of surface vestiture and sculpture, unless taxonomically or phylogenetically valuable, are not shown on illustrations. Homologous structures are drawn to the same scale (in most instances) and orientation to facilitate comparisons. Only taxonomically or phylogenetically valuable structures are illustrated; thus, comparisons of certain attributes of the structures for the purposes of identification may be misleading. Such attributes although illustrated for aesthetic completeness are not discussed in the text.

Distribution maps are presented for all species with the exception of *C. vibex*. Special maps and illustrations were prepared to illustrate general ecological and historical biogeographic patterns, evolutionary trends or adaptations, *etc.*, or as accompanying visual simplifications of various discussions in the text.

Hubbs-Hubbs diagrams representing intraspecific and interspecific variation in certain mensural attributes were prepared separately for each sex. Range, mean, 1.5 standard deviations (SD) on either side of the mean, and two standard errors (SE) on either side of the mean are plotted. Choice of 1.5 SD and 2 SE follows Whitehead (1971) as noted in the section on descriptive statistics.

Features illustrated are as follows: LEl, WRA/LR, WRA/WF, WElM/LEl, LP/LEl for *Stephanocleonus* (Figs. 49–53) and *Cleonidius* (Figs. 197–201); and, LEl, WRA/LR, WRA/WF, WElM/LEl, LP/LEl, WPT/WPB for *Apleurus* (Figs. 105–110). Features illustrated were selected on the basis of their taxonomic and/or phylogenetic value. Hubbs-Hubbs diagrams were also prepared to illustrate the altitudinal distributions of

Apleurus (Fig. 232) and *Cleonidius* (Fig. 233) species. Samples used for preparation of Hubbs-Hubbs diagrams minimally include those samples used in preparation of descriptive statistics tables. In those instances where measurements were taken of individuals from more than the sample used in the descriptive statistics tables, these other samples constituted part of an examination for possible intraspecific variation in mensural features.

Measurements and descriptive statistics.— Measurements were made on pinned specimens at various magnifications with the aid of an ocular micrometer in a Wild M5® microscope. Measurements selected for detailed study and for presentation were those that upon initial survey revealed differences between species of potential taxonomic or phylogenetic value. For this reason not all measurements or ratios presented were taken on species of all genera.

These measurements and their abbreviations are:

LR, length of rostrum measured in lateral aspect from anterior margin of eye to point of articulation of mandible; **WF,** minimum width of frons between eyes in dorsal aspect; **WRA,** maximum width of rostrum measured across apex in dorsal aspect; **LP,** length of pronotum measured along midline from anterior to posterior margins in dorsal aspect; **WPB,** width of pronotum measured across base in dorsal aspect; **WPT,** width of pronotum measured across apical one-third or one-quarter at tubercles (if present) or immediately posterior to sub-apical constriction in dorsal aspect; **WEIH,** width of elytra measured across base at humeri with elytra contiguous throughout length at suture in dorsal aspect; **WEIM,** width of elytra measured across midlength with elytra contiguous throughout length at suture in dorsal aspect; **LEI,** length of elytra measured along suture from apex of scutellum to apex of elytra in dorsal aspect; **LEy,** maximum length of eye measured in lateral aspect; **WEy,** maximum width of eye measured in lateral aspect.

Some of these measurements were used to obtain ratios which serve to express the form of a particular part of the body. These ratios are; WEy/LEy, shape of eye; WPB/LP, form of pronotum; WRA/LR, relative length of rostrum; WF/WRA, relative separation of eyes; WEIM/LEI, form of elytra; WP/LEI, relative length of elytra; and, WPT/WPB, position of maximum width of pronotum.

A comprehensive set of descriptive statistics is given for one sample of each species treated. (See Appendix 1, Tables 1–33). Statistical analysis is less comprehensive for those species where there was not adequate material. Sexes are treated separately and ideally each sample includes eight members of each sex collected at the same locality and time. This ideal is not met for all species and some samples have fewer than eitht specimens of one of the sexes or, for the purposes of more comprehensive statistical analysis, if markedly less than eight specimens are represented, are composed of a number of specimens collected from a more extensive geographic area. Least preferred samples are composed of all specimens of the species available for study. Mensural data treated in the descriptive statistics section include only those measurements and ratios given previously. Number of specimens, geographic locality of the specimens, range, mean, 1.5 standard deviations (SD), and 2 standard errors (SE) are given where number of specimens permits. In instances where too few specimens were available for meaningful statistical treatment, values for SD and SE are not given. Number of standard deviations and standard errors on either side of the mean were chosen following Whitehead (1971). Non-overlap of two standard errors from the mean is equivalent to a t-test at 0.05 probability, and indicates samples to be statistically significantly different; non-overlap of 1.5 standard deviations from the mean indicates that 90% or more of the specimens from one sample can be distinguished from 90% or more from the other sample, and indicates samples to

be taxonomically significantly different (Whitehead, 1971).

For most species these mensural features serve primarily as aids in identification and as characters valuable for phylogenetic analysis. For some species, mensural features are the primary, although not sole, criteria for species recognition. In these latter instances, the mensural features have been verified as reliable by further measurements taken on a larger number of specimens than that indicated in the descriptive statistics tables or on the Hubbs-Hubbs diagrams (*e.g.,* rostrum length in *C. texanus-C. longinasus*, form of elytra in *C. trivittatus-C. quadrilineatus*).

Analysis of geographic variation.— Where problems in species recognition were apparent in terms of geographic variation in structural features, population samples from sites throughout the species range were selected and examined to determine the taxonomic significance of this variation. If more or less extensive differences were found between samples, geographically intermediate samples (if available) were examined to infer the degree of reproductive isolation of the geographically more distant samples. Should geographically intermediate populations prove structurally intermediate between the two more distant samples, gene flow is inferred and all samples are considered conspecific. Divergence from both of the more distant samples or close similarity to any one of the two distant samples by the intermediate sample may indicate barriers to gene flow and may result in separate species status for the two most distant samples, particularly if geographically correlated with other variable structural features or aspects of natural history.

Descriptive format.— For each nomenclaturally valid taxon considered, a complete list of synonymy is given. Type material examined and depository are noted following each of the names of the nominal taxa. Lectotypes and neotypes are designated where appropriate; paralectotypes have not been designated. Complete label data for primary type material examined, type locality, gender, and type species are given where appropriate for species, subgenera and genera. All literature citations of names of North American species, *Cleonidius vibex* (Pallas), and all citations pertaining to *Cleonis pigra* (Scopoli) in North America are given. A concerted attempt has been made to make these listings as complete as possible. Page numbers have not been given for all citations, but only for those wherein new species are described. Published misidentifications ("misident." in synonymy list) are indicated under both the incorrect and correct names. Notes in parentheses following most literature references indicate the nature of that reference as follows: biol., biology; catal., catalog; check., checklist; desc., description; distn., distribution; and redesc., redescription. Lack of any notation indicates use of that name with little or no added information about the taxon.

For each species, subgenus or genus, a "Problems in recognition" section is presented which I feel to be more desirable than a diagnosis because the latter, in most instances, simply gives characters and their states already presented in the keys. In this section I discuss particular species that I had problems separating from, and perhaps at one time misidentified or confused with, the species in question. In this manner I point out the species with which others are likely to make errors. This section is meant to be consulted after a tentative identification has been made using the keys.

A section with notes about synonymy and type material follows and deals in various detail with specific criteria for newly proposed synonymy and with other details about type material as required. For all newly described species, label data for holotype and allotype are given in full with data from each label enclosed in separate quotation marks starting from the top label down. Separate lines on each label are indicated by a "/". A specific type locality is designated.

Paratypes are treated less rigorously and label information is given in a simple standard format of: locality, date, collector, sex, location of deposition. Specimens are ordered alphabetically according to locality. Derivation of the specific epithet is also given.

Following this section is a detailed description of the taxon including structural variation. Complementing this verbal description are various illustrations of important structural features and for all species, a set of variously comprehensive descriptive statistics from one population for each of males and females. Only attributes that vary between species are described. Character states are described in consistent order to facilitate comparisons. Subjective terms such as "large" and "small" have been avoided as much as possible but if by necessity used, are augmented with illustrations. All structural variation is incorporated in the appropriate places in the species description.

Geographic distribution of each species is presented in the form of dot maps illustrating positions of localities of collections. State records and questionable localities of collection are noted in the text but not placed on maps. Literature records are not placed on maps nor noted in text unless they fall outside the known range of the species based on other specimens examined. Complete lists of specimens examined for each species are not presented but have been placed in the Archives of the Department of Entomology, University of Alberta.

Natural history information from publications, specimen label data, and personal collecting experiences are summarized for each species. For the purposes of biogeographic and evolutionary interpretations, habitat associations were recognized using, as appropriate, schemes by Rzedowski (1978), Brown (1982), or Livingston and Shreve (1921). Elevations of collection localities are either taken directly from specimen labels (if noted), or, if site of collection is a major geographic feature, are taken from a gazetteer or one of a number of maps. Hubbs-Hubbs diagrams illustrate variation in elevational distribution within and among species of *Cleonidius* and *Apleurus* but no statistical tests are performed on these data. A Hubbs-Hubbs diagram is used only for the purpose of visual presentation of the altitudinal ranges. Seasonal data are taken from labels. Supra-generic classification of plants follows Cronquist (1968). Generic names of plants follow Kearney and Peebles (1960); species names follow Kearny and Peebles (1960), Munz and Keck (1968) and Correll and Johnston (1970).

Patterns of allopatry and sympatry for each species are summarized in the chorological relationships section. They are summarized for *Apleurus* and *Stephanocleonus* species, but presented in a table format for *Cleonidius* species. Consultation of this section not only reduces possible misidentifications in instances where specimen locality is known, but also indicates retention of species identity under variable conditions of species packing and species occurrence. For this reason special attention is given to chorological relationships with close phylogenetic relatives.

A section about phylogenetic relationships concludes the descriptive format and verbally states the immediate phylogenetic relationships of the taxon. For species of *Apleurus* and *Cleonidius*, further details are given in the "Phylogeny" section. Phylogenetic relationships have not been examined for species of *Stephanocleonus*.

For species groups of *Cleonidius*, only a short diagnosis and a statement of evidence for monophyly and phylogenetic relationships are presented. Structural features not variable within a species group but variable within *Cleonidius* are repeated in the species group diagnosis and all species descriptions.

Criteria for recognition of species-group taxa.— As with most systematists, my primary criterion for species recognition is the biological species concept (Mayr, 1963). I find the

evolutionary species concept of Wiley (1981), although theoretically desirable, so vague as to be of little practical applicability. Since experimental evidence of reproductive isolation is lacking for most insect species, Cleoninae being no exception, such isolation is inferred from differences primarily in structural features, but also in features of natural history, especially host plant associations.

In instances of sympatry, individuals are regarded as belonging to separate biological species if variable numbers of structural features are substantially and consistently different. Differing host plant associations alone are not evidence of separate species status, but in combination with differences in structural features are used herein to indicate separate species status. This consideration is especially important should the degree of structural difference be less than is found in sympatric species where host plant associations are broader or not consistently different yet structural differences are relatively extensive.

For allopatric individuals the situation is more complex and difficult to resolve. Allopatric individuals are regarded as conspecific if they exhibit structural features that do not differ, or if differing, do so to a lesser degree than differences noted between separate sympatric species and in a geographically based clinal manner. If the allopatric forms differ in various features of structure and/or natural history, and these features cannot be shown to have a consistent geographically determined pattern of continuous variation, the forms are considered separate species. Obviously, the more characters that differ in this manner, the more marked the evidence for separate species status. It is very important to note that marked phenetic differences are not the primary consideration, rather it is the pattern of geographic variation (assumed indicative of degree of gene flow) that determines the taxonomic status of the various populations. Phenetic differences may simply be the result of locally different selection pressures and not reproductive isolation.

These are my general criteria. Especially complicated and/or problematical patterns of structural variation must be considered individually and as such are discussed in detail in the text where appropriate.

The subspecific category has not been used. As expressed elsewhere (Anderson and Peck, 1986), I feel that this category should only be used for allopatric populations where lack of intermediate populations precludes analysis of geographic variation and inference of degree of reproductive isolation. In no instances in this study was such a consideration warranted; geographically intermediate populations and natural history information were consistently available to permit assessment of extent of gene flow and recognition of status at the species level.

Criteria for recognition of genus-group taxa with notes about classification.— Some consideration must be here given to criteria for recognition and ranking of genus-group taxa for this study is concerned with a regional fauna and classification of its constituents in terms of the world fauna. All genus-group taxa should preferably be monophyletic (holophyletic) although paraphyletic taxa are acceptable in certain special situations; polyphyletic taxa are not acceptable. Genus-group taxa should contain an assemblage of related species sharing structural features and/or features of natural history, and separated from other assemblages by a gap in such features. Aside from this requirement, naming and ranking of taxa are always debatable because there are no objective criteria for formal recognition of taxa, and if recognized, at what hierarchical level they should be placed. Although this has been attempted (Hennig, 1966), it has not met with widespread acceptance or success.

All decisions about naming and ranking must be made with reference to related taxa with genealogical and phenetic relationships of the taxa as the prime considerations. Genealogical relationships (including some consideration of confidence in them), should take priority over phenetic relationships because only classifications based on evolutionary parameters can logically contain more information, due to inheritance, than was initially used in their creation (Whitehead, 1972). Classifications of this nature may be maximally predictive and highest in information content, but may prove difficult to employ as information retrieval systems depending upon their complexity and intricacy. Many recent books (*e.g.,* Eldredge and Cracraft, 1980; Wiley, 1981; and references cited therein) have dealt with this problem at length and simple compromise between information content and facility for use is perhaps the most important general consideration in constructing classifications.

Four genera are recognized in this study as occurring in North America. *Cleonis* is monobasic; *Stephanocleonus* is represented in North America by only 6 species but in the Palearctic region by numerous species, so no intrageneric classification has been attempted (species in North America are herein arranged alphabetically); *Cleonidius* is represented by 20 species; 19 Nearctic, 1 Palearctic (at least); *Apleurus* is represented by 8 Nearctic species.

In *Cleonidius* only informal species groups, including the *incertae sedis* category, are recognized primarily because of low confidence in genealogical relationships and thus possible instability of the resultant classification, and little variation in structural features. By using only species groups, the possible predictive value of the classification is enhanced and can be tested without the problems associated with increased nomenclatural complexity, not desirable for such a small number of species of a relatively restricted geographic distribution.

In *Apleurus*, two subgenera have been recognized rather than species groups. Although *Apleurus* contains only eight species, the genealogically most primitive member of *Apleurus* differs from other species of *Apleurus* in a number of structural features, some not yet found elsewhere in Cleoninae. Confidence in this primitive phylogenetic position is high and structural differences are marked, with remaining *Apleurus* species forming a structurally cohesive grouping. For these reasons, recognition of subgenera was deemed desirable. Furthermore, desire for recognition of *Gibbostethus* as a subgenus is enhanced by the largely unknown natural history, restricted distribution, and possible endangered status of this phylogenetically most primitive species of *Apleurus*.

Classification above the generic level is not attempted, although some statements concerning relatives of genera occurring in North America and their shared character states are made, forming part of the basis for a future reclassification of the subfamily.

NATURAL HISTORY OF CLEONINAE

Members of the subfamily Cleoninae are found from mesic to very arid habitats. Taxa traditionally placed in the tribe Lixini are those usually associated with more mesic habitats whereas most traditional Cleonini are found in arid habitats. Exceptions, especially of some *Lixus* species associated with arid habitats, are known.

Most species breed in herbs or shrubs of a wide variety of plant taxa but most notably Chenopodiaceae, Compositae, Leguminosae, Rosaceae, Cruciferae and Polygonaceae. Larvae of most species mine stems or roots of these plants but those of some feed in flower heads or on seeds (*e.g., Rhinocyllus conicus, Larinus planus, Microlarinus* spp.). Natural history of *Microlarinus* spp. (Kirkland and Goeden, 1977; 1978a, b) and of *Rhinocyllus conicus* (Zwölfer

and Harris, 1984) have been particularly well studied; however, most other information about natural history of Cleoninae, especially in North America, is brief and fragmentary (*e.g.,* Bargagli, 1884; Pierce, 1907).

Adults of most species of traditional Cleonini are brachypterous and even those that are macropterous have not been observed to fly. Most traditional Lixini are macropterous.

Adults of various species have been collected as prey of *Bufo* sp. (Amphibia), *Geococcyx californicus* (Aves), and various predatory Hymenoptera. Tachinidae (Diptera) (Arnaud, 1978) and various parasitic Hymenoptera (Krombein *et al.*, 1979) have been recorded as parasites of members of the genus *Lixus* in North America.

Various species of Cleoninae have been employed as, or are being considered as, biological control agents of weeds including thistle (*Cirsium*, Compositae), knapweed (*Centaurea*, Compositae), and puncturevine (*Tribulus*, Zygophyllaceae) (Anderson, 1984a; Kirkland and Goeden, 1978a, b; Maddox, 1976; Wheeler and Whitehead, 1985; Zwölfer and Harris, 1984). None of the species are considered to be economic pests although some are occasionally found on cultivated Chenopodiaceae or Cruciferae.

SUPRASPECIFIC TAXA AND INCLUDED SPECIES

SUBFAMILY CLEONINAE

Historical review

As of 1978, 1445 species of Cleoninae had been described (O'Brien and Wibmer 1978). However, the number of genera stated is perhaps on the low side for many taxa given subgeneric rank under *Cleonus* likely require separate generic status. The subfamily name Cleoninae (first used as the vernacular "Cleonides") and generic name *Cleonus* were first proposed by Schoenherr (1826) but three years earlier, Schoenherr (1823) had also used the vernacular name "Geomorides" and the generic name *Geomorus* for the same taxa. Earlier still, Dejean (1821) had also proposed the name *Cleonis* to include species, some of which were subsequently placed by Schoenherr in *Geomorus* and *Cleonus*. Since Schoenherr (1823) used the vernacular name "Geomorides" and this was never latinized as Geomorinae, under Article 11f of the International Code of Zoological Nomenclature it is not a valid family-group name. Under Article 40, Cleoninae, even though the name of the type genus *Cleonus*, is a junior synonym, should not be replaced and is maintained as the valid family-group name. The name Cleoninae has been in widespread and constant use since its introduction (*e.g.,* Schoenherr, 1834; Chevrolat, 1873; Faust, 1904; Csiki, 1934; O'Brien and Wibmer, 1982).

North American species have traditionally been included in the tribe Cleonini (Casey, 1891; LeConte 1876a; LeConte and Horn, 1883) which is comparable to Cleoninae of other authors (*e.g.,* Csiki, 1934). There has been little confusion regarding included world taxa with the exception of the Holarctic genus *Lepyrus* now generally regarded not to be a cleonine.

Recognition of Cleoninae

Adults of the subfamily Cleoninae are recognized by two features not known in other Curculionidae. These are: 1), short, telescoping, ventrally situated, three-articled labial palpi; and 2), presence of paired symbiont sacs attached to the vagina near the base of gonocoxite II in females. A more detailed diagnosis describing other features of the subfamily is not presented, pending examination of further taxa.

Sex differentiation

Sexes are differentiated in Cleoninae as in most other weevils. Males are easily distinguished by flat to concave abdominal sterna III and IV and by possession of two clearly recognizable sclerotized terga at the abdominal apex, usually only visible upon displacement of the elytral apices. Females possess more evenly convex abdominal sterna III and IV and possess only a single sclerotized tergum at the abdominal apex. In addition, females tend to have a longer rostrum than do males (especially in *Cleonidius*) and are generally larger in body size.

Key to genera of New World Cleoninae

1   Rostrum, in dorsal view, from apex of epistoma to anterior margin of eye, more or less as long as greatest width (Figs. 1–2) 2

1′   Rostrum, in dorsal view, from apex of epistoma to anterior margin of eye, much longer than greatest width (Figs. 3–4, 10, 25–30, 81–88, 137–156) 4

2 (1)   Prosternum with a pair of prominent ridges which form a deep ventral channel . . . . *Bangasternus* Gozis
          (two species, one deliberately introduced, one under consideration for deliberate introduction)

2′   Prosternum lacking ridges, no channel evident 3

3 (2′) Elytron with intervals each with row of conspicuous erect setae. Anterolateral margin of pronotum straight, with long postocular vibrissae immediately behind eye (Fig. 1). Eye more or less round (Fig. 1) . . . . *Microlarinus* Hochhuth
          (two species, deliberately introduced)

3′   Elytron with intervals without row of erect setae. Anterolateral margin of pronotum with rounded postocular lobe and short postocular vibrissae behind eye (Fig. 2). Eye distinctly elongate-oval (Fig. 2) . . . .
          . . . . *Rhinocyllus* Germar
          (one species, deliberately introduced)

4 (1′) Pronotum dorsally and laterally with numerous shiny glabrous tubercles, lacking distinct punctures 5

4′   Pronotum dorsally and laterally distinctly punctate, with at most the outer margins of punctures of lateral margins swollen, glabrous and shiny 6

5 (4)   Rostrum dorsomedially sulcate throughout length (Fig. 10). Pronotum with anterolateral margins with rounded postocular lobe (Fig. 9) . . . .
          . . . . *Cleonis* Dejean, p. 449
          (one species, adventive)

5′   Rostrum dorsomedially carinate throughout length; lateral margins raised basally, appearing as lateral carinae. Pronotum with anterolateral margins straight, lacking rounded postocular lobe . . . . *Cyphocleonus* Motschulsky
          (one species, under consideration for deliberate introduction)

6 (4′) Mesosternum with mesosternal process markedly tumescent (Fig. 58). Male with aedeagus markedly expanded laterally from midlength to apical one-third (Fig. 97e) . . . *Apleurus* subgenus *Gibbostethus* Anderson, p. 468
          (one species, native)

6′   Mesosternum with mesosternal process flat or at most only slightly convex,

not tumescent (Fig. 59). Male with aedeagus more or less uniform in width
throughout median portion of length 7

7 (6') Tibia with corbel ridge rounded (Fig. 5). Elytron with all intervals equally
flat or with at most only humerus and very base of interval 3 swollen and
convex. Pronotum with disk with scale pattern various. Prosternum with or
without swellings; swellings, if present, situated immediately anterior to
each procoxal cavity (Fig. 8) 8

7' Tibia with corbel ridge sharp (Fig. 6). Elytron with all intervals equally flat
or with humerus and variously, sutural interval and intervals 3, 5, 7, and 9
elevated and convex throughout the greater part of their lengths. Pronotum
with disk with large white scales in lateral stripe of various width, small
and fine in moderately broad to very broad apically narrowed median
stripe; median area largely black in color, underlying dark cuticle not
obscured by overlying scales. Prosternum with or without swellings;
swellings, if present, situated immediately anterior to each prosternal
impression (Fig. 7) 10

8 (7) Antenna with article 2 of funiculus distinctly longer than wide, distinctly
longer than each of articles 3 to 6, slightly shorter than to distinctly longer
than article 1 (Fig. 4). Pronotum with anterolateral margins straight,
slightly sinuate, or with at most variously developed (usually small) acute
postocular projection; postocular vibrissae unequal in length, greatest
length (more or less equal to or greater than one-half width of eye) behind
base of eye (Fig. 4). Ventral surface of femur dentate or not. (Some South
American species of *Lixus* have slightly developed rounded postocular
lobes and moderately long postocular vibrissae of more or less equal length,
but have dentate femora) . . . . *Lixus* Fabricius
(numerous species, native; worldwide)

8' Antenna with article 2 of funiculus more or less as long as wide, more or
less subequal in length to each of articles 3 to 6, shorter than article 1
(Figs. 3, 137–156). Pronotum with anterolateral margins straight or with
slightly to well-developed, rounded postocular lobe; postocular vibrissae
uniformly short (less than one-half width of eye in length) to unequal in
length, greatest length (more or less equal to or greater than one-half width
of eye) behind base of eye (Figs. 3, 137–156). Femur not dentate 9

9 (8') Elytra elongate-narrow (width at midlength less than 0.65 times length)
(Figs. 118–136). Pronotal disk with distinct white scales of various sizes
(Figs. 118–136). Elytra with white scales, various in size, but more or less
obscuring view of underlying cuticle over large part of elytral surface (Figs.
118–136) . . . . *Cleonidius* Casey, p.492
(19 species, native; also in Palearctic Region)

9' Elytra more robust (width at midlength greater than 0.65 times length).
Pronotal disk with at most only very short indistinct setae, distinct scales
absent. Elytra with scattered patches of elongate fine scales in addition to
very short setae; underlying cuticle not obscured by scale cover . . . .
. . . . *Larinus* Schoenherr
(one species, introduced)

10 (7') Epistoma with anterior margin emarginate (Figs 25–30). Pronotum with well-developed, rounded postocular lobes; postocular vibrissae indistinct, uniformly short (Figs. 25–30). Eye elongate "kidney shaped" (Figs. 25–30); flat, or only slightly convex in dorsal view . . . .
. . . . *Stephanocleonus* Motschulsky, p. 453
(six species, native; also in Palearctic Region)

10' Epistoma with anterior margin rounded (Fig. 82–88). Pronotum with anterior margin straight behind eyes or with small acute postocular projection immediately behind base of eye; postocular vibrissae distinct and long, longest immediately behind base of eye (Figs. 82–88). Eye "teardrop shaped" (Figs. 82–88); protruding and moderately to markedly convex in dorsal view . . . . *Apleurus* subgenus *Apleurus* Chevrolat, p. 470
(seven species, native)

Ileomus Schoenherr is not given separate generic status in this key. Champion (1902–1906), although regarding it as a separate genus, states that "it is scarcely distinct from *Lixus*". Accordingly, individuals of species that are assigned to *Ileomus* by O'Brien and Wibmer (1982) key out in the above key to *Lixus*. Detailed study of phylogenetic relationships of the various groupings of *Lixus* species is needed to assess their validity as nominal subgeneric or generic taxa.

Genus *Cleonis* Dejean

Curculio; Scopoli 1763 (in part; sp. desc.). Linnaeus 1767 (in part; sp. desc.). Goeze 1777 (in part; sp. desc.). Knoch 1781 (in part; sp. desc.). Villers 1789 (in part; sp. desc.). Gmelin 1790 (in part; sp. desc.).
Cleonis Dejean 1821:96. Gender, feminine. Type species *Curculio sulcirostris* Linnaeus by subsequent designation (O'Brien and Wibmer 1982:73). Silfverberg 1979 (in part; check.). O'Brien and Wibmer 1982 (in part; catal., distn., misident. *Apleurus, Cleonidius, Stephanocleonus*). O'Brien and Wibmer 1984 (in part; misident. *Apleurus, Cleonidius, Stephanocleonus*).
Geomorus Schoenherr 1823: column 1141. Gender, masculine. Type species *Curculio sulcirostris* Linnaeus by original designation.
Cleonus Schoenherr 1826:145. Unjustified replacement name for *Geomorus* Schoenherr. Type species *Curculio sulcirostris* Linnaeus according to Article 67(h) of International Code of Zoological Nomenclature. Say 1831 (misident. *Cleonidius*). Kirby 1837 (misident. *Cleonidius*). LeConte 1850 (misident. *Stephanocleonus*). Melsheimer 1853 (misident. *Cleonidius*). LeConte 1858 (misident. *Apleurus*). LeConte 1859 (misident. *Apleurus*). Gemminger and von Harold 1871 (in part; misident. *Apleurus, Cleonidius*). LeConte 1876a (misident. *Cleonidius*). Henshaw 1881–1882 (misident. *Cleonidius*). LeConte and Horn 1883 (misident. *Cleonidius*). Henshaw 1885 (misident. *Cleonidius*). Wickham 1889 (misident. *Cleonidius*). Wickham 1896 (misident. *Cleonidius*). Fall 1897 (misident. *Cleonidius*). Fall 1901 (misident. *Cleonidius*). Wickham 1902 (misident. *Cleonidius*). Fletcher 1906 (misident. *Cleonidius*). Fall and Cockerell 1907 (misident. *Cleonidius*). Pierce 1907 (misident. *Cleonidius*). Ely 1913 (misident. *Cleonidius*). Gibson 1914 (misident. *Cleonidius*). Anderson 1914 (misident. *Cleonidius*). Blatchley and Leng 1916 (misident. *Cleonidius*). Yothers 1916 (misident. *Cleonidius*). Leng 1920 (misident. *Stephanocleonus, Apleurus, Cleonidius*). Leonard 1926 (misident. *Stephanocleonus, Cleonidius*). Böving 1927 (in part; larval key). Bradley 1930 (misident. *Apleurus, Cleonidius*). Crosby and Blauvelt 1930 (biol.). Leng and Mutchler 1933 (catal.). Wilcox *et al.* 1934 (misident. *Cleonidius*). Bleasdell 1937 (misident. *Stephanocleonus, Cleonidius*). Brimley 1938 (misident. *Cleonidius*). Brown 1940 (distn.). Blackwelder 1947 (misident. *Apleurus, Cleonidius*). Bruhn 1947 (misident. *Cleonidius*). Hicks 1947 (distn.). Hicks 1949 (distn.). Anderson 1956 (biol., distn.). Essig 1958 (misident. *Cleonidius*). Sanders 1960 (misident. *Cleonidius*). Kissinger 1964 (in part; biol.). Tanner 1966 (misident. *Apleurus, Cleonidius*). Kingsolver 1972 (misident. *Cleonidius*). Burke and Anderson 1976 (biblio.). Kumar *et al.* 1976 (misident. *Cleonidius*). Krombein 1979 (misident. *Stephanocleonus, Apleurus*). Arnett *et al.* 1980 (misident. *Cleonidius*). Batra *et al.* 1981 (distn.). Peschken 1984 (biol.).
Cleonus s.s.; Csiki 1934 (catal.).
Cleonus (*Cleonidius*); Arnett 1960–1962 (in part; misident. *Apleurus*).

Notes about synonymy.— *Epimeces* Billberg, 1820, p. 45, predates *Cleonis* Dejean, 1821 and originally included various Cleoninae (among others, *Curculio sulcirostris* Linnaeus, the type species of *Cleonis* Dejean, and, *Curculio filiformis* Fabricius, presently assigned to *Lixus* Fabricius [Csiki 1934]). The name *Epimeces*, to my knowledge, has not subsequently been used but because no type species has been designated for the genus, the name represents a threat to the priority of *Cleonis* Dejean. I therefore here designate *Curculio filiformis* Fabricius, 1781, p. 172, as the type species of *Epimeces* Billberg, 1820, p. 45. *Epimeces* therefore becomes a new junior subjective synonym of *Lixus* Fabricius, 1801, p. 498, type species *Curculio paraplecticus* Linnaeus, 1758, p. 380, by subsequent designation (Latreille, 1810, p. 430).

Schoenherr (1823), seeking consistency in gender of generic names, changed all feminine generic names in Curculionidae to a masculine name (not always the masculine form of the former feminine name). As a result of this, and according to Schoenherr (1823), inadequate characterization to recognize a type species, use of the name *Cleonis* Dejean, 1821 was discontinued, and the species initially placed in *Cleonis* were assigned to one of four genera by Schoenherr (1826). One of these was *Geomorus* Schoenherr, 1823. As such, *Geomorus* cannot be regarded as an express replacement name for *Cleonis*. Subsequently, Schoenherr (1826) proposed the genus *Cleonus* expressly as a replacement name (although unjustified) for *Geomorus* as indicated by his designation of *Curculio sulcirostris* Linnaeus, 1767 as the type species. This same species had already been designated by him as the type species of *Geomorus*. Schoenherr (1826) also placed all species initially included in *Geomorus* in *Cleonus*. The generic name *Cleonus* has since been in widespread use. However the name *Cleonis* was recently resurrected by Silfverberg (1979) and used by O'Brien and Wibmer (1982), Lohse (1983), and Wheeler and Whitehead (1985).

Cleonis Dejean is here used in a very restricted sense (subgenus *Cleonis* of Csiki [1934]) including only *C. pigra* (Scopoli), *C. japonicus* (Faust), and *C. sardous* (Chevrolat), the latter two species not examined by me. *Cleonis* appears closely related to *Cyphocleonus* Motschulsky and *Adosomus* Faust, and subsequent phylogenetic analysis may reveal the three to be congeneric.

Diagnosis.— Adult Cleoninae with moderately robust body form (Fig. 19). Rostrum with broad low median carina longitudinally sulcate throughout length (Fig. 10). Pronotum with small glabrous shiny tubercles, not distinctly punctate; pronotal postocular lobes slightly to moderately well-developed, rounded. Tibia with corbel ridge sharp (as in Fig. 6). Elytra with strial punctures individually indistinct, dorsal surface of elytra with scattered, small, irregularly shaped (usually transverse), glabrous, shiny swellings.

Description.— *Size.* Moderately large, moderately robust in form. *Mouthparts.* Prementum flat, with single large seta on each side. Maxillary palpus with palpifer and stipes each with large seta. Basal articles of labial palpi separated by distance subequal to width of a palpus. *Rostrum.* Moderately robust; with broad low median carina longitudinally moderately deeply sulcate throughout length from base of epistoma to base of frons; not medially tumescent (Figs. 9–10). Epistoma slightly swollen, with apical margin emarginate medially. Antenna with funiculus with article 1 very slightly longer than article 2 (Fig. 9); apical three articles of club with placoidal sensillae. *Head.* Eye elongate-quadrate, slightly wider at top than bottom; flat (Fig. 9). *Vestiture.* Dorsum lacking erect or suberect vestiture, with only simple elongate-narrow appressed white scales. Procoxae, mesocoxae, metasternum and base of abdominal sternum III of both sexes with moderately long suberect hair-like scales. *Prothorax.* Dorsal surface of pronotum with small glabrous shiny tubercles, not distinctly punctate. Median basal area shallowly impressed. Disk with elongate, moderately large, moderately dense, white scales present in broad lateral stripe and narrow median line, with scales small and fine in pair of paramedian apically narrowed stripes; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Fig. 19). Pronotum widest at base, lateral margins slightly rounded and convergent from base to apex; apical constriction very slight (Fig. 19). Pronotal postocular lobes rounded, slightly to moderately well-developed (Fig. 9). Prosternum with slight impression anterolaterad of each procoxal cavity and with slight swelling immediately anterior to each prosternal impression. *Legs.* Tarsi broad, articles 2 and 3 more or less as broad as long, subequal in length; article 1

only slightly longer than articles 2 or 3; article 3 deeply bilobed (Fig. 18). Ventral tarsal pilosity extensive, covering entire ventral surface of articles 1 to 3 (Fig. 18). Claws connate in basal one-third, not to slightly divergent. Foretibia with small to moderately well-developed second spur; inner margin with moderately large denticles throughout greater portion of length. Tibia with corbel ridge sharp. Metatibia of male with uncus with ventral margin slightly sinuate. *Wings.* Present. *Elytra.* Base of interval 3 and humerus very slightly swollen and convex, otherwise intervals uniformly flat. Humeri distinct. Strial punctures individually indistinct, dorsal surface of elytra with scattered small irregularly shaped (usually transverse) glabrous shiny swellings. *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed scale. *Genitalia.* Female. Abdominal sternum VIII lacking basal arm (Fig. 17). Gonocoxite II elongate-triangular, apex not prolonged into marked lobe; stylus moderately large, apical in position (Fig. 15). Spermathecal gland slightly elongate-oval (Fig. 16). Male. Aedeagus elongate, moderately robust; in lateral view, moderately arcuate near base then only slightly arcuate throughout rest of length (Fig. 13). Apex slightly spatulate. Internal sac with median dorsal pocket high; various lobes present; apical and dorsal median pockets individually distinct; apical sclerite complex present, individual sclerites distinctly scythe-like (Figs. 11, 12, 14).

Comparisons.— As noted, *Cleonis* species are very similar to those of *Adosomus* and *Cyphocleonus* in that all possess a pronotum and elytra that are distinctly tuberculate and not punctate. *Adosomus* and *Cleonis* species possess moderately well-developed, rounded, postocular lobes, whereas postocular lobe are lacking from *Cyphocleonus* species. The only feature which distinguishes *Cleonis* from both of these two genera is the medially longitudinally sulcate rostrum of the former. In *Adosomus* the rostrum is medially tumescent and not carinate or sulcate, whereas in *Cyphocleonus* species, the rostrum is variously medially tumescent and carinate. *Cyphocleonus trisulcatus* (Herbst) has a low broad median carina but which is only apicomedially sulcate.

Checklist of included species.— Following Csiki (1934), three species are recognized. They are *C. japonicus* (Faust), *C. sardous* (Chevrolat), and *C. pigra* (Scopoli). *Cleonis pigra* is the only one of the three species that I have examined and is the only one that occurs in the Nearctic Region.

Faust (1904) distinguishes *C. pigra* and *C. japonicus* from *C. sardous* by the latter having metatarsal article 2 slightly longer than article 3 and by differences in the pronotal scale patterns. *Cleonis pigra* and *C. japonicus* are separated on the basis of extent of distribution and development of the pronotal and elytral tubercles, the distribution of the ventral abdominal glabrous patches, and body shape. Based upon examination of only Nearctic representatives of *C. pigra*, I find all of these characters vary somewhat, and suspect that the three included species may prove conspecific.

Phylogenetic relationships.— *Cleonis, Cyphocleonus* and *Adosomus* appear to represent a monophyletic group based on the presence of a tuberculate rather than punctate pronotum and elytra. Beyond this, affinities of the group are uncertain.

Cleonis pigra (Scopoli)
(Figs. 9–19, 213)

Curculio piger Scopoli 1763:23.
Curculio sulcirostris Linnaeus 1767:617.
Curculio transversofasciatus Goeze 1777:409.
Curculio nebulosus Knoch 1781:87 [not Linnaeus 1758:385].
Curculio fasciatus Villers 1789:216 [not Müller 1776:86].
Curculio fasciatus Gmelin 1790:1804.
Cleonis sulcirostris; Dejean 1821.
Cleonus sulcirostris; Gyllenhal 1834.
Cleonus indicus Fåhraeus 1842:55.
Cleonus piger; Everts 1903.

Cleonis piger; Silfverberg 1979 (check.). O'Brien and Wibmer 1982 (catal., distn.).
Cleonis pigra; O'Brien and Wibmer 1984.

Notes about synonymy.— The synonymical list follows Csiki (1934); I have not examined type material of this species or of any of its conspecific forms. This is the species frequently referred to in previous publications as *C. sulcirostris*.

Description.— *Specimens examined.* 61 unsexed. *Size.* Length, male, 7.5–13.4 mm; female, 11.4–14.8 mm. Width, male, 3.7–6.6 mm; female, 5.8–7.0 mm. *Rostrum.* Lateral margins sharp, indicated by low rounded carina from above point of antennal insertion to frons (Fig. 10). Side portion of rostrum immediately ventrad of lateral carina moderately deeply sulcate from immediately anterior to eye to point of antennal insertion; with moderately deep elongate-narrow punctures, most linearly confluent or nearly so. *Prothorax.* Surface dorsally and laterally with numerous small shiny glabrous tubercles; medially with small to large elongate-oval shiny glabrous swelling. Prosternum in lateral view with apical portion flat, slightly shorter than adjacent posterior steeply declivous portion. *Elytra.* Sutural interval in basal one-half, intervals 2 to 5 basally, and two obliquely posteromedially directed patches (at basal one-third from intervals 2 to 5 and at apical one-third from intervals 2 to 4) with small irregular slightly elevated shiny glabrous patches (Fig. 19). *Wings.* Long (greater than elytra in length). Bases of 2A joined but very lightly sclerotized. *Abdomen.* Ventral surface with small shiny glabrous patches distinct and dense on abdominal sterna III and IV, less distinct on sterna V to VII. *Genitalia.* Female (2 specimens). Abdominal sternum VIII with lateral arms narrow, evenly and slightly inwardly arcuate throughout length, expanded apically (Fig. 17). Male (2 specimens). Aedeagus robust; in lateral view narrowed from approximately apical one-third to apex (Fig. 13). Internal sac with single, large, broad, dorsally directed, lobe; with moderately large, paired, laterally directed, lobes and small dorsally directed median lobe on dorsal surface at midlength; with small dorsolaterally directed paired lobes at midlength and midheight (Figs. 11–12). Eversible apical sclerite complex with paired scythe-like sclerites, each with median elongate-narrow projection long, visible in lateral view (Figs. 11, 14); adjacent ventral surface and basal portion of sides of apex of sac with pair of large transverse dark sclerites (Fig. 11).

Geographic distribution.— This species was accidentally introduced into North America from Europe prior to 1919, the year of the earliest known North American record (Anderson, 1956). It occurs throughout New York and southern Ontario, west to Michigan and east to eastern Quebec and New Brunswick (Fig. 213). It is widespread in the Palearctic Region (Csiki, 1934).

Variation.— As part of a program investigating the potential for use of *C. pigra* as a biological control agent for the introduced *Centaurea diffusa* Lam. (diffuse knapweed) in the prairie provinces of Canada, a study of variation based on 15 mensural features was carried out on adult individuals of *C. pigra* reared from species of *Cirsium*, *Carduus* and *Centaurea* (all Compositae) to determine if structurally distinct host races exist (Anderson, 1984a). Measurements were made of 15 characters and a linear discriminant analysis was performed. Separation using the generated discriminant function proved unreliable and because absolute size was the principal component upon which the function was based, it was concluded that only a single polyphagous morphotype was present. Differences in absolute size are likely a result of structural attributes of the different larval feeding and pupation sites in the different host plants and are doubtfully heritable.

Natural history.— Anderson (1956) summarizes information about the natural history of this species in North America as follows. Adults are the overwintering stage and are first found on Canada thistle, *Cirsium arvense* (L.) Scop., or bull thistle, *Cirsium vulgare* (Savi) Tenore, in early June. Copulation and oviposition take place through mid-July. Eggs are laid singly in the lower portions of the stems in cavities chewed by the females and subsequently plugged with frass following deposition of the egg. Larvae bore downward into the primary root where they feed for approximately 30 days. Pupation takes place in the root. Adults emerge in August or September and overwinter under ground debris. Although a wide range of Compositae serve as host plants in Europe (Anderson, 1956; Peschken, 1984, and references cited therein), only two plants, *Cirsium arvense* and *Cirsium vulgare*, both adventive, are known to serve as hosts in North America (Anderson 1956). Native North American *Cirsium* species or other Compositae are not attacked by the weevils.

A similar range of host plant associations to those of *C. pigra* in Europe is also found in another species of Cleoninae, *Rhinocyllus conicus* Froelich, which was recently shown to consist of various host specific races (Zwölfer and Preiss, 1983). As such, host plant races are also suspected in *C. pigra* although, as noted, an examination of the structural features of adults reared from various Compositae did not reveal differences between individuals reared from different plant taxa.

Immature stages were described by La Ferla (1939).

Genus *Stephanocleonus* Motschulsky

Cleonus; LeConte 1850 (in part). Leng 1920 (in part; catal.). Leonard 1926 (in part; check.). Bleasdell 1937 (in part). Krombein 1979 (in part; as prey).

Stephanocleonus Motschulsky 1860:540 (in key). Gender, masculine. Type species *Curculio flaviceps* Palliser by original designation. LeConte 1876a (key, sp. descs.). Henshaw 1881–1882 (in part; check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Blatchley and Leng 1916 (key, sp. redesc.).

Coniocleonus Motschulsky 1860:540 (in key). NEW SYNONYMY. Gender, masculine. Type species *Cleonus carinirostris* Gyllenhal by original designation.

Plagiographus Chevrolat 1873:21. Gender, masculine. Type species not designated.

Cleonus (*Stephanocleonus*); Casey 1891 (in part; key). Fall and Cockerell 1907 (in part; check.). Csiki 1934 (in part; catal.). Arnett 1960–1962 (in part; catal., key). Kissinger 1964 (in part; key).

Cleonis; O'Brien and Wibmer 1982 (in part; catal., distn.). O'Brien and Wibmer 1984 (in part).

Notes about synonymy.— The genera *Stephanocleonus* and *Coniocleonus* were both originally proposed by Motschulsky (1860). They were distinguished by the rostrum having only a single median carina in the latter, whereas in *Stephanocleonus*, the rostrum, in addition to the median carina, also had a smaller oblique carina on each side. *Stephanocleonus* is also noted as being apterous but nothing is said of the state of the wings in *Coniocleonus*. I have examined specimens of *Stephanocleonus flaviceps* Palliser, the type species of *Stephanocleonus*, and, in the single male available, did not see small oblique lateral carinae, but only a single uniformly steeply declivous median carina. The two females examined have the median carina similarly steeply declivous basally but decreasingly declivous apically. A very slight oblique carina is present where this more gradual apical declivity meets the flat surface of the rostrum on each side of the median carina. All three individuals are wingless.

I have not seen specimens of *Coniocleonus carinirostris* Gyllenhal, the type species of that genus, but I have examined a male and a female of each of *C. excoriatus* Gyllenhal and *C. glaucus* Fabricius, a female of *C. cineritius* Gyllenhal, and a male of each of *C. cinerascens* Hochhuth and *C. ferrugineus* Fåhraeus. Individuals of *C. excoriatus* and *C. glaucus* are macropterous and the rostrum has a single median carina which is gradually declivous throughout its length. There are no small lateral carinae evident. However, the specimens of *C. cineritius*, *C. cinerascens* and *C. ferrugineus* each have a rostrum with slightly to moderately well-developed oblique lateral carinae in the same position as in the females of *S. flaviceps*, and have wings of variable length.

In view of this variation and the lack of other distinguishing characters, I cannot accept other than that *Stephanocleonus* is simply an apterous *Coniocleonus*. I do not think the rostral differences between the type species warrant separate generic status. I therefore consider *Stephanocleonus* and *Coniocleonus* to be new subjective synonyms, a decision anticipated by Casey (1891:188) who stated, regarding the Nearctic species, that "It is a question whether our species should be placed in *Stephanocleonus* or *Plagiographus* [a junior synonym of *Coniocleonus* according to Faust, 1904 and Csiki, 1934], but this is a matter of but slight importance as the differences between the subgenera appear to be very inconsiderable".

I choose to give the name *Stephanocleonus* priority over *Coniocleonus* because the former has been the only name used in reference to the Nearctic species here placed in the genus. Furthermore, no major works have recently appeared dealing with *Coniocleonus*, however, a recent review by Ter-Minasyan (1979) of the *Stephanocleonus* of the Palearctic Region includes species that in my opinion are congeneric with species in North America.

Diagnosis.— Adult Cleoninae with moderately robust to robust body form (Figs. 20–23). Eye kidney-shaped, flat (Figs. 25–30). Rostrum with well-developed sharp median carina (Figs. 25–30). Pronotum punctate; pronotal postocular lobes well-developed, rounded; postocular vibrissae uniformly short (Figs. 25–30). Meso- and especially metatarsus elongate-narrow, with all articles markedly longer than broad; article 2 distinctly longer than article 3; article 1 markedly longer than articles 2 or 3. Tibia with corbel ridge sharp (as in Fig. 6). Procoxae, mesocoxae, metasternum, metacoxae and base of abdominal sternum III of male with moderately long to very long erect hair-like scales; hair-like scales sparse to lacking in female. Pronotal disk with elongate, white, moderately large, moderately dense scales present in lateral stripe of various width, small and fine in moderately broad to very broad, apically narrowed, median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 20–23). Prosternum with or without swellings, swellings, if present, immediately anterior to each prosternal impression (as in Fig. 7). Metauncus of male with ventral margin slightly to markedly sinuate. Female with abdominal sternum VIII with basal arm very long (Figs. 37–42); gonocoxite II rounded basally, with apex prolonged into a marked lobe (Fig. 54). Male with apex of aedeagus spatulate or not (Figs. 31–36); internal sac with or without large paired sclerite at midlength (Figs. 31–36).

Description.— *Size.* Moderately large, moderately robust to robust in body form (Figs. 20–23). *Mouthparts.* Prementum ventrally longitudinally carinate, slightly swollen to flat, with one or more large setae on each side. Maxillary palpus with palpifer and stipes each with at least one large seta. Bases of labial palpi separated by distance subequal to width of basal article of labial palpus. *Rostrum.* Moderately to markedly robust, not medially tumescent; with low to high, sharp median carina (Figs. 25–30). Epistoma markedly swollen or not, with apical margin emarginate medially (Figs. 25–30). Antenna with funiculus with article 1 slightly to markedly longer than article 2 (Figs. 25–30); apical three articles of club with placoidal sensilla. *Head.* Eye kidney-shaped, flat (Figs. 25–30). Upper margin of eye rounded to sharp, frons convex to markedly concave. *Vestiture.* Dorsum lacking or with at most only very short indistinct suberect or erect vestiture, with simple elongate-narrow appressed white scales of various size and density. Procoxae, mesocoxae, metasternum, metacoxae and base of abdominal sternum III of male with moderately long to very long erect hair-like scales; hair-like scales sparse to lacking from female. *Prothorax.* Dorsal surface of pronotum punctate. Pronotum with median basal area shallowly to deeply impressed, disk with or without various other impressions. Disk with elongate white moderately large moderately dense scales present in lateral stripe of various width, small and fine in moderately broad to very broad apically narrowed median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 20–23). Pronotum widest at base to subequal in width from base to apical one-quarter, then constricted to various extent and convergent to apex (Figs. 20–23). Pronotal postocular lobes moderately to well-developed, postocular vibrissae uniformly short (length less than one-half maximum width of eye) (Figs.; 25–30). Prosternum with slight impression anterolaterad of each procoxal cavity; with or without slight swelling immediately anterior to each prosternal impression (as in Fig. 7). *Legs.* Foretarsus moderately broad, articles 2 and 3 more or less subequal in length, at most slightly longer than broad; article 1 only slightly longer than articles 2 or 3; article 3 moderately deeply bilobed. Meso- and especially metatarsus elongate-narrow; all articles markedly longer than broad, article 2 distinctly longer than article 3; article 1 markedly longer than articles 2 or 3, article three slightly bilobed. Ventral tarsal pilosity various in extent, lacking entirely on at least more basal articles in most species. Claws connate in basal one-third, not to slightly divergent. Foretibia with inner margin near apex with moderately-developed subapical tooth, inner margin with at most only small denticles in apical one-half. Metatibia of male with uncus with ventral margin slightly to markedly sinuate. Tibia with corbel ridge sharp. *Wings.* Absent or present (various in length). *Elytra.* Intervals flat to variously slightly swollen and convex; striae distinctly punctate. Humeri acute to rounded. Dorsal surface of most species with variously developed, posteromedially directed oblique patches of small and fine scales at each of basal one-third and apical one-third to midlength (Figs. 20, 22–23). *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed scale. Sternum VII of male with apex variously medially emarginate in most species. *Genitalia.* Female. Abdominal sternum VIII with long basal arm

(Figs. 37–42). Gonocoxite II rounded basally, with apex prolonged into marked lobe; stylus moderately large, apical in position (Fig. 54). Spermathecal gland round (Fig. 48). Male. Aedeagus robust and short to elongate-narrow, various in shape in lateral view; apex not to markedly spatulate (Figs. 31–36). Internal sac various; median pocket low, apical and dorsal median pockets individually distinct or not, various lobes present; apical sclerite complex with individual sclerites distinctly scythe-like, large paired sclerite at midlength present or absent (Figs. 43–48).

Comparisons.— *Stephanocleonus* is very similar to *Pleurocleonus* however, the latter lacks pronotal postocular lobes, has an elongate-teardrop-shaped eye, tarsal claws that are widely divergent, and a low broad longitudinally sulcate median rostral carina. Species of *Stephanocleonus* may also be confused with *Nomimonyx* and *Epirhynchus* because of similarities in head and rostral form, and eye shape. *Epirhynchus* however, has a single tarsal claw, and both have short broad tarsal articles, not the markedly elongate-narrow articles of *Stephanocleonus* species.

Although unlikely, some *Conorhynchus, Bothynoderes* and *Chromonotus* may also be confused with *Stephanocleonus* species. These taxa however have article 2 of the antennal funiculus longer than article 1; in *Stephanocleonus* species, article 1 is longer than article 2.

Checklist of included species.— In the Nearctic Region, six species are placed in *Stephanocleonus*. Numerous species occur in the Palearctic Region (Csiki 1934; Ter-Minasyan 1979) but are not listed here. The six Nearctic species are as follows:

1. *S. confusus* Anderson, n. sp.
2. *S. cristaticollis* Csiki
3. *S. immaculatus* Anderson, n. sp.
4. *S. parshus* Anderson, n. sp.
5. *S. plumbeus* (LeConte)
6. *S. stenothorax* Anderson, n. sp.

Phylogenetic relationships.— Distribution of the apotypic character state of female gonocoxite II (rounded basally and with a marked apical lobe [Fig. 54]) suggests that *Stephanocleonus, Pleurocleonus* Motschulsky, *Menecleonus* Faust, *Xanthochelus* Chevrolat, and *Conorhynchus* Motschulsky (= *Temnorhinus* Chevrolat) form a monophyletic group. *Menecleonus, Xanthochelus* and *Pleurocleonus* appear to further comprise another monophyletic group (based upon presence of an unpaired sclerite near the confluence of the apical pocket and the dorsal median pocket in the internal sac of the aedeagus of males) that is the sister-group of *Stephanocleonus*. This proposed sister-group relationship is based of article 1 of the antennal funiculus being longer than article 2. *Conorhynchus* has article 2 of the funiculus longer than article 1 and is likely the sister-group to the *Stephanocleonus-Pleurocleonus, Menecleonus, Xanthochelus* lineage. *Bothynoderes* Schoenherr, *Chromonotus* Motschulsky and also *Chromosomus* Motschulsky, have the apotypic state of elongate-narrow meso- and metatarsi and together with the above taxa likely comprise another monophyletic group based upon shared possession of this character state. They also have a very similar "elongate-teardrop" eye-shape to *Conorhynchus* and similarly all have article 2 of the antennal funiculus longer than article 1.

Key to species of adult *Stephanocleonus*

1   Dorsal surface of elytra uniformly covered with small white scales, without distinct maculations; with or without small shiny glabrous area at confluence of intervals 4 to 6 (Fig. 21). Elytra with humeri distinct; lateral margins more or less straight in basal one-half (Fig. 21) . . . .
————————————————— . . . . *S. immaculatus* Anderson, p. 460

1′   Dorsal surface of elytra faintly to distinctly maculate, with small white
         scales less dense in two posteriorly directed oblique patches (one at basal
         one-third from intervals 2 to 6; the other at apical one-third from intervals
         2 to 4), and with small triangular shiny glabrous area at confluence of
         intervals 4 to 6 (Figs. 20, 22–23). Elytra with humeri less distinct or
         rounded; lateral margins more or less arcuate in basal one-half (Figs. 20,
         22–23)   2

2   (1′) Elytra fused together; thoracic wings short, approximately equal to
         one-half length of elytra   3

2′   Elytra not fused together; thoracic wings long, approximately equal to or
         greater than length of elytra   4

3   (2)   Elytra with scattered small recurved hair-like scales, most evident on
         declivity from sutural interval to interval 3; with greater part of length of
         sutural interval and intervals 3 and 5 elevated and convex. Female with
         sternum VII flat, lacking paired tumescence. Male with median lobe
         elongate; apex slightly spatulate; in lateral view narrowed from apical
         one-third to apex; with at most small basal ventral tubercle (Fig. 31) . . . . .
         . . . . *S. confusus* Anderson, p. 457

3′   Elytra lacking erect hair-like scales, with only the extreme base of interval
         3 convex, otherwise with all intervals flat throughout their length. Female
         with ventral surface of sternum VII with paired tumescence. Male with
         median lobe less elongate; apex markedly spatulate; in lateral view,
         narrowed from approximately midlength to apex; with large basal ventral
         tubercle (Fig. 32) . . . .*S. cristaticollis* Csiki, p. 459

4   (2′) Pronotum with subapical constriction well-defined dorsally and laterally,
         with distinct moderately deep impressions laterad of median carina at
         apical one-quarter laterally continuous with subapical constriction; with
         apical margin broadly and moderately deeply emarginate at middle. Elytra
         with tubercle at confluence of intervals 4 to 6 markedly elevated. Rostrum
         robust (width at apex greater than 0.90 times length); approximately
         uniform in width throughout length (Fig. 30) . . . .
         . . . . *S. stenothorax* Anderson, p. 465

4′   Pronotum with subapical constriction only laterally well-defined, lacking or
         with at most only very shallow indistinct impressions laterad of median
         carina; with apical margin not or only very slightly emarginate at middle.
         Elytra with tubercle at confluence of intervals 4 to 6 only slightly elevated.
         Rostrum more elongate-narrow (width at apex less than 0.90 times length);
         slightly narrowed at midlength (Figs. 28–29)   5

5   (4′) Pronotum with punctures large, deep and dense, distance between
         punctures distinctly less than diameter of a puncture (Fig. 28). Female
         metatarsal article 3 with large ventral pilose pads. Male with median lobe
         in ventral view with apex symmetrical (Fig. 34b); internal sac lacking
         median dorsal pocket and large dorsally directed paired lobes on dorsal
         surface immediately anterior to midlength (Fig. 46) . . . .

. . . . *S. parshus* Anderson, p. 461

5′   Pronotum with punctures small, shallow and sparse, distance between punctures greater than diameter of a puncture (Fig. 29). Female metatarsal article 3 entirely spinose, lacking ventral pilose pads. Male with median lobe in ventral view with apex asymmetrical (Fig. 35b); internal sac with median dorsal pocket and without dorsally directed lobes from dorsal surface (Fig. 47) . . . . *S. plumbeus* (LeConte), p. 464

Stephanocleonus confusus Anderson, new species
(Figs. 20, 25, 31, 37, 43, 204)

Stephanocleonus plumbeus; LeConte 1876a (in part; desc., misident., mixed type series). Henshaw 1881–1882 (in part; check., misident.). Henshaw 1885 (in part; check., misident.). Wickham 1902 (check., misident.). Wickham 1909 (check., misident.). Leng 1919 (in part; check., poss. misident.). Leng 1920 (in part; catal., misident.). Danks 1981 (in part; check., poss. misident.).
Cleonus cristatus; Casey 1891 (key, misident.).
Cleonus (Stephanocleonus) plumbeus; Fall and Cockerell 1907 (in part; check., misident.).
Stephanocleonus cristatus; LeConte 1878 (distn., misident.). Leng 1920 (in part; catal., misident.).
Cleonus plumbeus: Krombein 1979 (in part; prey, poss. misident.).
Cleonis cristaticollis; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).
Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, labelled with a red label "HOLOTYPE", "Spearfish Canyon/ Black Hills, S.D./ 15–18:VI:1910.", inverted "*Cleonus/ cristatus/* Lec.", "HOLOTYPE/ *Stephanocleonus/ confusus/* Anderson" and with abdomen on card and genitaliain microvial attached to pin (USNM). Allotype, female, labelled with red label "ALLOTYPE", "Tp.21 Rge.6/ W.4 Mer. Alberta/ 12.V.1980/ Lot 3 BF&JL Carr", "ALLOTYPE/ *Stephanocleonus/ confusus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Spearfish Canyon, Black Hills, South Dakota.

Paratypes. 37 males, 29 females. CANADA: Alberta: Township 1, Range 4, West 4 Meridian, 23.V.82, B.F. and J.L. Carr, 1M (RSAN); Township 13, Range 14, West 4 Meridian, 16.IV.82, B.F. and J.L. Carr, 1M (JLCC); Township 14, Range 25, West 4 Meridian, 15.V.82, B.F. and J.L. Carr, 1F (JLCC); Township 10, Range 2, West 5 Meridian, 11.V.82, B.F. and J.L. Carr, 1F (RSAN); Township 30, Range 21, West 4 Meridian, 17.IV.82, B.F. and J.L. Carr, 1M (RSAN); Medicine Hat, 22.IV.29, F.S. Carr, 1F (UASM), 13.VI.32, F.S. Carr, 2M, 1F (UASM), 24.VI.30, F.S. Carr, 1F (UASM), 27.III.27, F.S. Carr, 1F (UASM), 14.IV.26, F.S. Carr, 1F (UASM), 13.VI.33, F.S. Carr, 1F (UASM), 2.VII.23, F.S. Carr, 1M (UASM), 11.V.32, F.S. Carr, 1M (UASM), 13.V.27, F.S. Carr, 1M (RSAN), 13.V.23, F.S. Carr, 1M (UASM), 6.IX.27, F.S. Carr, 1F (UASM), 12.VII.24, F.S. Carr, 1F (RSAN), 18.II.24, F.S. Carr, 1F (UASM), 8.V.65, J.L. Carr, 1F (JLCC); Township 14, Range 13, West 4 Meridian, 22.VII.79, J.L. Carr, 1M (JLCC); Ghost Dam, 2.VII.80, B.F. and J.L. Carr, 1F (JLCC); Seebe, 7.VI.73, B.F. and J.L. Carr, 1M (JLCC); Suffield, 20.IV.23, 1F (UASM); Township 6, Range 1, West 4 Meridian, 20.V.80, B.F. and J.L. Carr, 1F (JLCC); Township 10, Range 2, West 5 Meridian, 28.IV.81, B.F. and J.L. Carr, 1M (JLCC); Township 15, Range 14, West 4 Meridian, 9.V.80, B.F. and J.L. Carr, 1F (JLCC); 27mi. sw. Nordegg, 13.VI.66, R. Frietag/T.L. Erwin, 1F (CWOB); Calgary, IV.11, Criddle, 1F (CNCI); Lethbridge, 6.V.30, J.H. Pepper, 1M (CNCI). Northwest Territories: 1M (CNCI). Saskatchewan: Township 6, Range 2, West 3 Meridian, 13.VIII.73, B.F. and J.L. Carr, 1M (RSAN); Cypress Hills Provincial Park, 29.V.63, Cook *et al.*, 1F (CNCI).

UNITED STATES OF AMERICA: Arizona: Coconino County, 2.4mi. n. Kaibab Lodge, 28.VII.71, Lawton/Willis, 2M (CWOB). Colorado: Grant/Jackson County, Rabbit Ears Pass, 2872 me., 19.VI.81, M. Kaulbars, 1M (RSAN); Top of Range below Sapello and Pecos Rivers, 11,000 ft., 1.VIII.00, H.F. Wickham, 1M (USNM); Cumbres Pass, 10,000 ft., 22.VI.35, E.C. Van Dyke, 1M (CASC); 1mi. n. Nederland, 11.VIII.73, C.W. O'Brien, 1M (CWOB); Longs Peak, 10–11,000 ft., 8.VII.26, E.C. Van Dyke, 1M (CASC); Argentine Road, H.F. Wickham, 1M (USNM); Kenosha Pass, 16.VII.38, J.W. Green, 1F (CASC); Gore Pass, 15.IX.48, O. Bryant, 1F (CASC); Leadville, 7–14.VII.96, H.F. Wickham, 1M (USNM). Montana: Helena, Hubbard and Schwarz, 2M (USNM); Flathead Lake, 12.VII.11, 1F (USNM); Gallatin County, 9.IV.32, 1M (MSU), 8.V.32, 1F (MSU), 1VI.31, 1F (MSU); Bozeman, 17.V.28, 1M (MSU), 11.V.25, 1M (MSU); 15mi. ne. Bozeman, 30.VI.72, Burleson, 1M (MSU); 6mi. e. Dell, 30.VI.54, Anderson, 1M (MSU). Nevada: White Pine County, 17.7mi. n., 3.5mi. nw. McGill, Monte Neva Hot Springs, 25.VII.71, Lawton and Willis, 1M, 1F (CWOB). New Mexico: 1F (MCZ); Cloudcroft, V.18, 1M (CASC). Utah: Alta, 29.VI.47, O. Bryant, 1F (CASC). Wyoming: 1F (USNM); Beulah, 21.VII., T.D.A. Cockerell, 1M (UASM); Park County, Beartooth Plateau, 6.VII.61, S.M. Sutton, 1M (UCM), 31.VIII.59, J.G. Edwards, 1F (CWOB); Beartooth Plateau, Hairgrass Canyon, 7.VII.59, 1F (CWOB); Bighorn Mountains, Medicine Mountain, 18.VIII.62, J.G. Edwards, 1F (CWOB); Tie Siding, VIII.25, 1F (USNM).

Notes about synonymy.— An individual of this species from New Mexico was included in the original type series of *S. plumbeus* LeConte. *Stephanocleonus plumbeus* as herein recognized does not occur in New Mexico.

Derivation of specific epithet.— From the Latin "*confusio*" meaning mixed or confused. This name is used in reference to the previous confusion of this species with *S. plumbeus.*

Problems in recognition.— This is the only species of North American *Stephanocleonus* in which the elytra have small recurved hair-like scales on the dorsal surface and in which elytral intervals 3 and 5 are markedly elevated and convex throughout the greater part of their lengths. The internal sac of the male aedeagus is also distinctive (Fig. 43).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 1. *Size.* Length, male, 9.2–15.0 mm; female, 10.5–14.8 mm. Width, male, 4.7–6.5 mm; female, 4.9–7.2 mm. *Head.* Frons with punctures large, sparse, shallow, not confluent; also with small broad appressed white scales, dense laterally, sparse medially. Some specimens with slightly raised carina on vertex. *Rostrum.* Moderately robust, slightly more so in males (width at apex 0.85-0.95 times length in male; 0.810-0.909 in female) (Fig. 25). With well-developed, sharp, steeply declivous, low, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, moderately deep fovea (Fig. 25). Rostrum flat from immediately laterad of median carina to lateral margins, lateral margins sharp from above point of antennal insertion to anterior margin of eye, indicated in few specimens by slightly raised rounded carina. Dorsal punctures large, sparse, shallow, not confluent. With scales small broad appressed white, dense laterally, sparse medially. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With low broad indistinct median carina in anterior one-half. Subapical constriction well defined laterally, not so dorsally; some specimens with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area narrowly, moderately deeply impressed. Dorsal punctures moderately large to large, dense and moderately deep; medially, distance between punctures markedly less than diameter of single puncture, some punctures confluent and irregularly impressed; laterally, the distance between punctures subequal to or greater than diameter of an individual puncture. *Prosternum.* With shallow impression anterior to each procoxal cavity, and with slightly to moderately developed transverse swelling anterior to each impression. *Elytra.* Robust in general form (width at midlength 0.64-0.72 times length in male; 0.62–0.71 in female) (Fig. 20). In dorsal view with lateral margins evenly arcuate from midlength to base, humerus rounded, not distinct (Fig. 20). Sutural interval and intervals 3 and 5 (in some specimens also basal one-half of interval 7) elevated and convex throughout the greater part of their lengths. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, the other at apical one-third from intervals 2 to 4. With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6 (Fig. 20). With scattered very short recurved hair-like scales, most evident on declivity from sutural interval to interval 3. *Wings.* Short (more or less equal to one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small to moderately large, indistinct to distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate-narrow pads on apical one-quarter of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from article 1, lacking to present as elongate-narrow pads on apical one-quarter to one-half of article 2, as elongate-oval pads on apical one-half of article 3; of mesotarsus of male, lacking to as apical tufts on outer lobe of article 1, as elongate-narrow pads on apical three-quarters on outer lobe and as apical tufts on inner lobe of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of female, lacking from article 1, lacking from to as elongate-narrow pads on apical one-half on outer lobe of article 2, as small to large elongate-oval pads on apical one-third to two-thirds of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical one-quarter to three-quarters of article 3; of metatarsus of female, lacking from articles 1 to 3 to as elongate-oval pads covering apical one-third of article 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms narrow, slightly inwardly and evenly arcuate throughout length (Fig. 37). Male (12 examined). Abdominal sternum VIII with paired sclerite with inner apices truncate (Fig. 31c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex symmetrical, medially produced into acuminate apical projection (Figs. 31a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with large dorsally directed paired lobe on dorsal surface at apical one-third; median dorsal pocket high, with large laterally directed paramedial lobes at basal one-third near ventral margin (Fig. 43). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 43a).

Geographic distribution.— This species is known from southern Alberta and southern Saskatchewan, south to Arizona and New Mexico (Fig. 204). Most published records of *S. cristaticollis* refer to this species.

Natural history.— Adults of this species have been collected in prairie habitats in southern Alberta to alpine habitats at elevations of 3400 m in Colorado and New Mexico.

Chorological relationships.— This species is broadly sympatric with *S. cristaticollis* and *S. parshus*, and narrowly sympatric with *S. immaculatus* along the western limits of the range of the latter.

Stephanocleonus cristaticollis Csiki
(Figs. 26, 32, 38, 44, 205)

Stephanocleonus cristatus LeConte 1876a:147 [not Chevrolat 1873:98]. Holotype (examined), female, labelled "Utah", "*S./cristatus/* Lec", "Horn Coll/ H8514" and with my label indicating it as the holotype "*Stephanocleonus/ cristatus* LeConte/ HOLOTYPE labelled/ by Anderson" (MCZC). Type locality, Utah. LeConte 1878 (distn., misident. of *S. confusus*). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Leng 1920 (in part; catal., misident. *Stephanocleonus confusus*).
Cleonus (*Stephanocleonus*) *cristatus*; Casey 1891 (key, misident. *Stephanocleonus confusus*). Csiki 1934 (catal.).
Cleonus (*Stephanocleonus*) *cristaticollis* Csiki 1934:26. New name for *Stephanocleonus cristatus* LeConte.
Cleonis cristatus; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).
Cleonis cristaticollis; O'Brien and Wibmer 1982 (in part; catal., distn., misident. *Stephanocleonus confusus*).

Problems in recognition.— This is one of two brachypterous species of North American *Stephanocleonus*. Unlike *S. confusus* individuals, in which elytral intervals 3 and 5 are elevated and convex throughout the greater part of their lengths, individuals of *S. cristaticollis* have only the extreme base of interval 3 slightly elevated and convex. They also do not possess the short recurved hair-like scales on the dorsal surface of the elytra that are found in *S. confusus*. Abdominal sternum VII of females has a pair of low rounded swellings, and the shape of the male aedeagus and form of the internal sac are distinctive (Figs. 32, 44).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 2. *Size.* Length, male, 13.8 mm; female, 13.6–14.1 mm. Width, male, 6.4 mm; female, 6.4–6.6 mm. *Head.* Frons with punctures large, sparse, shallow, indistinct; also with small elongate appressed white scales, dense laterally, sparse medially. *Rostrum.* Moderately robust (width at apex 0.86 times length in male; 0.91 in female) (Fig. 26). With well-developed, sharp, steeply declivous, low, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, moderately deep fovea (Fig. 26). Rostrum with shallow trough immediately laterad of median carina, lateral margins sharp from above point of antennal insertion to anterior margin of eye, indicated by slightly raised rounded carina. Dorsal punctures large, sparse, shallow, indistinct. With scales small, elongate, appressed, white, dense laterally, sparse medially. *Pronotum.* Dorsal apical margin shallowly emarginate at middle. With low broad indistinct median carina in anterior one-half. Subapical constriction well defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area broadly, moderately deeply impressed. Dorsal punctures small, sparse and shallow; medially and laterally with distance between punctures subequal to or greater than diameter of single puncture; punctures irregularly impressed and dense in median basal area. *Prosternum.* With only shallow impression anterior to each procoxal cavity. *Elytra.* Moderately robust in general form (width at midlength 0.63 times length in male; 0.65 in female). In dorsal view with lateral margins evenly arcuate from midlength to base, humerus rounded, not distinct. Base of interval 3 swollen and convex, otherwise elytral intervals uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, the other at apical one-third from intervals 2 to 4. With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Short (more or less equal to one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate-oval pads on apical one-third of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from article 1, present as apical tufts of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-quarter of outer lobe, lacking from inner lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on more or less entire ventral surface of article 3; of mesotarsus of female, lacking from articles 1 and 2, as elongate-narrow pads covering apical three-quarters of article 3; of metatarsus of male, lacking from articles 1

and 2, as elongate-oval pads on apical three-quarters of article 3; of metatarsus of female, lacking from articles 1 to 3. *Abdomen.* Abdominal sternum VII in female with pair of rounded swellings at midlength; in male with apical margin slightly emarginate medially. *Genitalia.* Female (one examined). Abdominal sternum VIII with basal arm slightly expanded at apex; lateral arms broad, slightly inwardly and evenly arcuate throughout length (Fig. 38). Male (two examined). Abdominal sternum VIII with paired sclerite with inner apices acuminate (Fig. 32c). Aedeagus moderately robust; in lateral view markedly arcuate, more so in basal one-half, narrowed gradually from midlength to apex, apex markedly spatulate; in ventral view with apex symmetrical, medially produced into elongate rounded apical projection (Figs. 32a,b). Base of aedeagus with large ventral tubercle (Fig. 32a). Internal sac globose with dorsally directed median lobe on dorsal surface; with moderately large dorsolaterally directed paired lobe at midlength near dorsal margin (Fig. 44). In lateral view with basal paired sclerite and apical sclerite complex approximate (Fig. 44a).

Geographic distribution.— This species is known from only four specimens: two males and a female from southern Alberta (Medicine Hat, Monarch, Gorge Creek), and the female holotype from Utah (no further locality data given) (Fig. 205). Most published records of this species refer to *S. confusus.*

Chorological relationships.— The distribution of the few known specimens indicates that this species is probably broadly sympatric with *S. confusus* and narrowly sympatric with western *S. parshus.*

Stephanocleonus immaculatus Anderson, new species
(Figs. 21, 27, 33, 39, 45, 202)

Cleonus (*Stephanocleonus*) *plumbeus*; Fall and Cockerell 1907 (in part; check., misident.). Csiki 1934 (in part; catal., misident.).

Stephanocleonus plumbeus; Blatchley and Leng 1916 (in part; key, redesc., misident.). Leng 1919 (in part; check., poss. misident.). Leng 1920 (in part; catal., misident.). Danks 1981 (in part; check., poss. misident.).

Cleonus plumbeus; Leonard 1926 (in part; check., poss. misident.). Krombein 1979 (in part; prey, poss. misident.).

Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "McMurray,/ Alta. V.10.53/ W.J. Brown", "HOLOTYPE/ *Stephanocleonus/ immaculatus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Allotype, female, with a red label "ALLOTYPE", "Gillam Man./ 10.VI.1949/ J.B. Wallis", "ALLOTYPE/ *Stephanocleonus/ immaculatus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Fort McMurray, Alberta.

Paratypes. 10 males, 16 females. CANADA: Alberta: Township 93, Range 10, West 4 Meridian, 1.VI.85, B.F. and J.L. Carr, 1F (JLCC); McMurray, 21.VI.53, W.J. Brown, 1F (CNCI), 29.VII.53, G.E. Ball, 1M (RSAN), 22.VI.53, G.E. Ball, 1F (CNCI); Lac La Biche, NE shore, 30.VI.63, L.M. Kenakin, 1F (CWOB); Township 37, Range 18, West 5 Meridian, 18.VII.73, B.F. and J.L. Carr, 1F (RSAN); Township 35, Range 18, West 5 Meridian, 18.VIII.67, B.F. and J.L. Carr, 1F (JLCC); Exshaw, 27.VI.54, B.F. and J.L. Carr, 1M, 1F (JLCC); High Prairie, 26.VII.61, A.R. Brooks, 1F (CNCI). British Columbia: Canal Flats, 13.V.82, B.F. and J.L. Carr, 1M (RSAN). Manitoba: Gillam, 16.VI.50, F. McAlpine, 1F (CNCI); Aweme, 31.V.10, N. Criddle, 1F (USNM); Beaujou [sic], 24.VI.61, H.E. Milliron, 1M (CNCI). Northwest Territories: Fort Smith, 17.V.50, J.B. Wallis, 1F (CNCI), 16.VI.50, W.G. Helps, 1F (CNCI). Ontario: Lake Superior, Whitefish Point, 46°38'N 84°33'W, Hubbard and Schwarz, 1M, 1F (USNM). Saskatchewan: Junction Highways 2 and 165 east, 22.VI.85, B.F. and J.L. Carr, 1M, 1F (JLCC); Hudson Bay, 9.VII.54, Brooks-Wallis, 1M, 1F (CNCI).

UNITED STATES OF AMERICA: Colorado: Douglas County, 19.IV.15, 1M (CASC). Minnesota: 1F (USNM). Nebraska: Lincoln, 29.VI., Wolcott, 1F (UNSM). South Dakota: Englewood, Haggard, 1M (UNSM).

Derivation of specific epithet.— From the Latin "*im*" meaning not, and "*macula*" meaning spot or mark. This name is used in reference to the lack of distinct elytral markings in most individuals of this species.

Problems in recognition.— This is the only species of North American *Stephanocleonus* in which the elytra are more or less uniformly covered with small white scales and in which most specimens lack a distinct pattern of elytral maculations (Fig. 21). Most specimens also lack the small triangular shiny glabrous area at the confluence of intervals 4 to 6 which is found in all other North American *Stephanocleonus* (Fig. 21). The shape of the male aedeagus and form of the internal sac are also distinctive (Figs. 33, 45).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 3. *Size.* Length, male, 13.3–15.6 mm; female, 14.8–16.8 mm. Width, male, 5.9–6.8 mm; female, 6.8–7.5 mm. *Head.* Frons with punctures large, moderately dense, moderately deep, many punctures longitudinally confluent, appearance longitudinally rugose; also with small broad appressed white scales, sparse laterally, absent to very sparse medially. Most specimens with slightly raised carina on vertex. *Rostrum.* Moderately robust, slightly more so in females (width at apex 0.80-0.95 times length in male; 0.79-0.96 in female) (Fig. 27). With well-developed, sharp, steeply declivous, high, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, moderately deep fovea (Fig. 27). Rostrum flat from immediately laterad of median carina to lateral margins, lateral margins rounded to sharp from above point of antennal insertion to anterior margin of eye. Dorsal punctures large, moderately dense, moderately deep, many punctures confluent. With scales small uniformly dense, elongate-narrow appressed, white. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With low broad distinct median carina in anterior one-half. Subapical constriction slightly to well defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area narrowly, shallowly impressed. Dorsal punctures moderately large, dense and moderately deep; medially, the distance between punctures less than diameter of individual puncture, some punctures confluent or nearly so and irregularly impressed; laterally, distance between punctures subequal to diameter of individual puncture. *Prosternum.* With only very shallow impression anterior to each procoxal cavity. *Elytra.* Moderately robust in general form (width at midlength 0.58-0.68 times length in male; 0.56-0.67 in female) (Fig. 21). In dorsal view with lateral margins straight, slightly convergent from slightly past midlength to base, humerus acute, very distinct (Fig. 21). All elytral intervals more or less flat. Scales white, small, dense, no distinct maculations present (Fig. 21). Some specimens with a slightly elevated, small, triangular, glabrous, shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth moderately large, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male elongate-narrow pads on apical one-quarter to one-half of article 1, as large elongate-oval pads on apical three-quarters to more or less entire ventral surface of articles 2 and 3; of female, pilose vestiture lacking from article 1, as apical tufts to elongate-narrow pads on apical one-half of article 2, as elongate-oval pads on apical three-quarters of article 3; of mesotarsus of male, lacking from, to as an elongate-narrow pad on apical one-third of outer lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on apical three-quarters to more or less entire ventral surface of article 3; of mesotarsus of female, lacking from article 1, lacking from, to as elongate-narrow pad on apical one-half of outer lobe of article 2, as large elongate-oval pads on apical two-thirds of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-narrow pads on apical two-thirds of article 3; of metatarsus of female, lacking from articles 1 and 2, as apical tufts to small elongate-oval pads on apical one-half of article 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (five examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms broad, inwardly arcuate at midlength (Fig. 39). Male (six examined). Abdominal sternum VIII with paired sclerite with inner apices rounded (Fig. 33c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex symmetrical, medially produced into truncate apical projection (Figs. 33a,b). Base of aedeagus with at most small ventral tubercle (Fig. 33a). Internal sac elongate with small laterally directed paired lobe near ventral margin at or slightly beyond midlength; median dorsal pocket high, with large dorsolaterally directed paired lobe at basal one-third near ventral margin, separated from base of median pocket by distinct trough (Fig. 45). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 45a).

Geographic distribution.— This species is known from widely scattered localities in the southwestern Northwest Territories, northern Manitoba, and central Ontario, south in the west to Colorado and Nebraska (Fig. 202).

Natural history.— A single adult has been collected on *Rosa* sp. (Rosaceae).

Chorological relationships.— his species is broadly sympatric throughout the northern part ofits range with *S. plumbeus* and *S. parshus*, and is narrowly sympatric in the western part of its range with *S. confusus*.

Stephanocleonus parshus Anderson, new species
(Figs. 28, 34, 40, 46, 203)

Cleonus (*Stephanocleonus*) *plumbeus*; Casey 1891 (key). Csiki 1934 (in part; catal., misident.). Kissinger 1964 (biol., misident.).
Stephanocleonus plumbeus; Blatchley and Leng 1916 (in part; key, redesc., misident.). Leng 1919 (in part; check., poss.

misident.). Leng 1920 (in part; catal., misident.). Marcovitch 1923 (biol., redesc., larvae, misident.). Danks 1981 (in part; check., poss. misident.).
Cleonus plumbeus; Leonard 1926 (in part; check., poss. misident.). Bleasdell 1937 (check., prob. misident.). Krombein 1979 (in part; prey, poss. misident.).
Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "Chalk River, Ont./ May 16, 1938/ N.R. Brown", "HOLOTYPE/ *Stephanocleonus*/ *parshus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Allotype, female, with a red label "ALLOTYPE", "Tp. 36 Rge. 15/ W.5 Mer Alberta/ 16.VII.1973/ B&J Carr Lot 3", "ALLOTYPE/ *Stephanocleonus*/ *parshus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Chalk River, Ontario.

Paratypes. 39 males, 43 females. CANADA: Alberta: Township 24, Range 8, West 5 Meridian, 8.VII.82, B.F. and J.L. Carr, 1M (RSAN); Bragg Creek, 31.V.75, F.A.H. Sperling, 1M, 1F (RSAN); Pincher Creek, 20.VI.61, H.E. Milliron, 1M (CNCI); McMurray, 4.VI.53, W.J. Brown, 1M (CNCI), 6.VI.53, W.J. Brown, 1F (CNCI); Township 25, Range 3, West 5 Meridian, 7.VI.73, B.F. and J.L. Carr, 2M (JLCC, RSAN); Township 29, Range 5, West 5 Meridian, 28.VI.64, B.F. and J.L. Carr, 1M (JLCC); Calgary, 28.VI.64, B.F. and J.L. Carr, 1M (RSAN); Exshaw, 27.VI.54, B.F. and J.L. Carr, 1M (JLCC), 19.V.60, J.L. Carr, 1M (JLCC); Willow Creek, 9.VIII.28, H. Richmond, 1M (CASC); Ghost Dam, B.F. and J.L. Carr, 1F (JLCC); Edmonton, 26.V.19, F.S. Carr, 1M, 1F (UASM), 14.V.20, F.S. Carr, 1F (UASM), 13.V.18, F.S. Carr, 1M (UASM); Medicine Hat, 13.VI.32, F.S. Carr, 2M, 1F (UASM); Crow's Nest Pass, 9.VI.30, J.H. Pepper, 1M (CNCI); Beaverlodge, 1F (UASM); near Josephburg, 53°41'N 113°55'W, 23.V.79, K. Shaw and J. Sutcliffe, 1F (UASM). British Columbia: Rolla, 21.VII.27, Vroom, 1F (CASC); Pouce Coupe, 1.VII.27, Vroom, 1F (CASC); Baynes Lake, 9.V.76, B.F. and J.L. Carr, 1F (JLCC); Canal Flats, 13.V.82, B.F. and J.L. Carr, 1M, 1F (JLCC); Skookumchuck, 30.V.84, B.F. and J.L. Carr, 1M (JLCC). Manitoba: Aweme, 12.VIII.29, R.H. Handford, 1F (RSAN), 2.VII.29, N. Criddle, 1M (CNCI), 20.IV.06, N. Criddle, 1F (CNCI), 31.V.10, N. Criddle, 1F (USNM), 9.VI.14, N. Criddle, 1M, 1F (CNCI), 24.IX.28, N. Criddle, 1M (CNCI), VI, N. Criddle, 1M (USNM), 1.VII.05, N. Criddle, 1F (USNM), V.12, N. Criddle, 1M (USNM), 3.VIII., N. Criddle, 1F (USNM); Township 14, Range 105, 12.V.24, J.B. Wallis, 1F (CNCI); Riding Mountain National Park, 12.VI.38, W.J. Brown, 1F (CNCI); Melita, 8.VI.20, N. Criddle, 1F (CNCI); Shell River, VII.27, E. Criddle, 1F (CNCI); Winnipeg, 1F (USNM); Treesbank, 24.VI.48, Criddle, 1F (CNCI); Sandilands, 22.VI.30, W.J. Brodie, 1F (CNCI); 24km. w. Haddashville, 27.VI.84, I. Askevold, 1M (CWOB). Northwest Territories: Fort Wrigley, 27.IX.29, O. Bryant, 1M (CASC); Fort Simpson, Manners Creek, 11.VI.72, Smetana, 1F (CNCI). Ontario: Blackburn, 6.VI.32, W.J. Brown, 1F (CNCI); Ridgeville, VI.35, S.D. Hicks, 1F (CNCI); Toronto, 1M (USNM); Dunrobin, 18.V.77, J.E. O'Hara, 1M (RSAN). Quebec: Kazubazua, 25.V.33, W.J. Brown, 1M (CNCI); Fort Coulonge, 25.VI.19, J. Beaulne, 1M (CNCI). Saskatchewan: 8mi. e. Saskatoon, 17.VI.73, C.K. Starr, 1F (CWOB); Township 35, Range 6, West 3 Meridian, 20.VII.85, B.F. and J.L. Carr, 1M (JLCC); Pike Lake, 5.I.42, King & Glen, 1F (CNCI); Prince Albert, 4.VII.54, Brooks-Wallis, 1F (CNCI).

UNITED STATES OF AMERICA: Connecticut: New Hartford, 26.IV.20, Zappe, 1F (CWOB). Iowa: Ames, 1F (USNM). Maine: 1M (USNM). Massachusetts: Woodshole, 1F (CASC). Michigan: Emmet County, Mackinaw City, 28.VI.20, M.H. Hatch, 1M (USNM). Minnesota: 1F (CASC); Crow Wing County, Pelican Lake, 25.VIII.10, Wolcott, 1F (USNM), 28.VIII.08, Wolcott, 1F (USNM). Montana: Missoula, 16.V.04, 1F, 11.VII.04, 1M (USNM); Helena, Hubbard and Schwarz, 1F (USNM); Flathead County, Echo Lake, 31.V.35, Eichmann, 1F (MSU); Hamilton, 16.VIII.26, 1M (MSU); Lake County, 6.VII.36, 1M (MSU). Nebraska: Lincoln, VI., 1F (UNSM); Bellevue, 20.V.02, Bruner, 1M (UNSM). New Mexico: 1F (MCZC). South Dakota: Englewood, Haggard, 1F (UNSM). Tennessee: Knoxville, 12.IV.55, H. and A. Howden, 1F (HAHC), 17.V.57, H. and A. Howden, 1M (HAHC). Vermont: Bennington County, G.H. Horn, 1M (USNM); Lyndon, 22.VIII.00, Melander, 1M, 1F (OCUC).

Country unknown: Bridge, 31.V.14, 1F (CNCI).

Derivation of specific epithet.— An arbitrary combination of letters.

Problems in recognition.— Among macropterous North American *Stephanocleonus* species with elytral maculations, individuals of *S. parshus* can be recognized by the large deep and dense pronotal punctures, the distance between punctures distinctly less than the diameter of a puncture (Fig. 28a). As in individuals of *S. plumbeus*, the pronotum has the lateral subapical constriction not defined dorsally and has the apical margin entire and not emarginate. In addition to other features, females of *S. parshus* can further be distinguished from those of other North American macropterous species by the metatarsus with article 3 with elongate pilose pads; males can be distinguished from males of other species by the distinctive shape of the aedeagus and form of the internal sac (Figs. 34, 46).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 4. *Size.* Length, male, 10.4–12.0 mm; female, 10.9–13.6 mm. Width, male, 4.8–5.6 mm; female, 5.0–5.9 mm. *Head.* Frons with punctures large, dense, moderately deep, many punctures confluent, appearance longitudinally rugose; also with small elongate-narrow appressed

white, dense scales. Most specimens with slightly raised carina on vertex. *Rostrum.* Moderately elongate-narrow, slightly more so in males (width at apex 0.76-0.84 times length in male; 0.77-0.84 in female) (Fig. 28). With well-developed, sharp, gradually declivous, high, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, shallow fovea (Fig. 28). Rostrum rounded to flat from immediately laterad of median carina to lateral margins, lateral margins rounded to sharp from above point of antennal insertion to anterior margin of eye, indicated in very few specimens by slightly raised rounded carina. Dorsal punctures large, moderately dense, moderately deep, many confluent. With scales small, elongate-narrow, appressed, white, dense. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With low, broad, distinct median carina in anterior one-half. Subapical constriction slightly to well defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area narrowly, shallowly impressed. Dorsal punctures large, dense and deep; medially, most confluent and irregularly impressed; laterally, distance between punctures much less than diameter of individual puncture (Fig. 28a). *Prosternum.* With shallow impression anterior to each procoxal cavity, and with or without slightly developed transverse swelling anterior to each impression. *Elytra.* Moderately robust in general form (width at midlength 0.61-0.68 times length in male; 0.59-0.65 in female) (Fig. 22). In dorsal view with lateral margins straight and convergent from midlength to base, humerus obtuse, distinct. All elytral intervals more or less uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, other at apical one-third from intervals 2 to 4. With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (equal to or greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small to moderately large, indistinct to distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-half of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from article 1, present as elongate-oval pads on apical one-half of article 2, as elongate-oval pads on more or less entire ventral surface of article 3; of mesotarsus of male, lacking from to present as an apical tuft of outer lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on more or less entire ventral surface of article 3; of mesotarsus of female, lacking from article 1, lacking from to present as an elongate-narrow pad on apical one-half of outer lobe of article 2, as large elongate-oval pads on more or less entire ventral surface of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical one-third to one-half of article 3; of metatarsus of female, lacking from articles 1 and 2, as an elongate-oval pad on apical one-third to one-half of outer lobe and apical one-half to two-thirds of inner lobe of article 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (three examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms narrow, inwardly arcuate at midlength (Fig. 40). Male (12 examined). Abdominal sternum VIII with paired sclerite with inner apices rounded (Fig. 34c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex symmetrical, medially produced into rounded apical projection (Figs. 34a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with large dorsally-directed paired lobe on dorsal surface immediately beyond midlength; median dorsal pocket lacking, with large dorsolaterally directed paired lobe at basal one-third near dorsal margin (Fig. 46). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 46a).

Geographic distribution.— This species is widely distributed in North America from Maine and Massachusetts south to Tennessee, west to Nebraska and Iowa in the south, British Columbia and Alberta in the north (Fig. 203). A single state record for New Mexico is in the Horn collection at the Museum of Comparative Zoology, Harvard University.

Natural history.— At Knoxville, Tennessee, Marcovitch (1923) records larvae of this species feeding on roots of strawberry in June, July, December and March. Pupae were found on July 13 and a single adult emerged on July 25. Although identified as *S. plumbeus*, the description provided notes that the thorax is coarsely punctured. This, and the verified occurence of only *S. parshus* at Knoxville, indicates that this is the species to which he referred.

Chorological relationships.— This, the most widespread species of North American *Stephanocleonus*, is sympatric in the northern part of its range with *S. plumbeus*; in the northeastern part of its range with *S. immaculatus*; and, in the western part of its range with *S. cristaticollis* and *S. confusus*.

Stephanocleonus plumbeus LeConte
(Figs. 22, 29, 35, 41, 47, 205)

Cleonus obliquus; LeConte 1850 (check., misident.).

Stephanocleonus plumbeus LeConte 1876a:146. Lectotype (here designated), male, one of an undetermined number of syntypes, labelled with a pale blue circle (=Lake Superior), "Type/ 5259", and with card with abdomen attached, microvial containing genitalia, and my designation label "*Stephanocleonus/ plumbeus* LeC./ LECTOTYPE/ desig. Anderson" (MCZC). Type locality, north shore of Lake Superior. LeConte 1876a (in part; desc., misident. *Stephanocleonus confusus*, mixed type series). Henshaw 1881–1882 (in part; check., misident. *Stephanocleonus confusus*). Henshaw 1885 (in part; check., misident. *Stephanocleonus confusus*). Wickham 1902 (check., misident. *Stephanocleonus confusus*). Wickham 1909 (check., misident. *Stephanocleonus confusus*). Blatchley and Leng 1916 (in part; key, redesc., misident. *Stephanocleonus immaculatus, Stephanocleonus parshus*). Leng 1919 (in part; check., poss. misident. *Stephanocleonus immaculatus, Stephanocleonus parshus, Stephanocleonus confusus, Stephanocleonus stenothorax*). Leng 1920 (in part; catal., misident. *Stephanocleonus immaculatus, Stephanocleonus parshus, Stephanocleonus confusus*). Marcovitch 1923 (biol., redesc., larvae, misident. *Stephanocleonus parshus*). Danks 1981 (in part; check., poss. misident. *Stephanocleonus immaculatus, Stephanocleonus parshus, Stephanocleonus confusus, Stephanocleonus stenothorax*).

Cleonus (Stephanocleonus) plumbeus; Casey 1891 (key). Fall and Cockerell 1907 (check., misident. *Stephanocleonus immaculatus, Stephanocleonus confusus*). Csiki 1934 (in part; catal., misident. *Stephanocleonus immaculatus, Stephanocleonus parshus, Stephanocleonus confusus*).

Cleonus plumbeus; Leonard 1926 (in part; check., poss. misident. *Stephanocleonus immaculatus, Stephanocleonus parshus*). Bleasdell 1937 (check., poss. misident. *Stephanocleonus parshus*). Kissinger 1964 (biol., misident. *Stephanocleonus parshus*). Krombein 1979 (in part; as prey, poss. misident. *Stephanocleonus immaculatus, Stephanocleonus parshus, Stephanocleonus confusus*).

Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident. *Stephanocleonus immaculatus, Stephanocleonus parshus, Stephanocleonus confusus*).

Problems in recognition.— Among North American *Stephanocleonus* species that are macropterous and possess maculated elytra, this species can be recognized by the following combination of characters: pronotum with lateral subapical constriction not defined dorsally; apical margin of pronotum entire, not emarginate at middle; and pronotal punctures small, shallow and sparse, distance between punctures greater than diameter of individual puncture (Fig. 29a). Females of this species have the metatarsus with article 3 lacking ventral pilose pads.

Individuals of this species are most likely to be confused with those of *S. parshus*, but the two can be readily separated by characters noted in the key and above.

Notes about synonymy.— I have been unable to ascertain the exact constitution of the type series of *S. plumbeus* LeConte. The species was described from an unspecified number of specimens from the north shore of Lake Superior and from New Mexico. In the LeConte collection at the Museum of Comparative Zoology, there are three specimens labelled as types; two specimens with pale blue circles attached (= Lake Superior), and a single specimen labelled "N.M." (= New Mexico). I have selected one of the two Lake Superior specimens as lectotype and believe that these three specimens likely initially constituted the type series of *S. plumbeus*. The other specimen from Lake Superior is conspecific with the lectotype, but the specimen labelled "N.M." is *S. confusus*.

Other specimens in the LeConte and Horn collections, but not labelled as types and therefore questionably part of the type series, include one of *S. immaculatus* with no locality data; two of *S. plumbeus* with no locality data; and one of *S. parshus* from New Mexico.

Description.— *Specimens examined.* 13 males, 11 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 5. *Size.* Length, male, 10.9–13.0 mm; female, 11.2–15.6 mm. Width, male, 4.9–6.0 mm; female, 5.2–7.2 mm. *Head.* Frons lacking distinct large punctures; uniformly covered with small elongate-narrow appressed white scales. Some specimens with slightly raised carina on vertex. *Rostrum.* Moderately elongate-narrow to moderately robust, (width at apex 0.82–0.90 times length in male; 0.82–0.94 in female) (Fig. 29). With well-developed, sharp, gradually declivous, high, median carina from above point of antennal insertion to base of rostrum; basally terminated at small, shallow fovea

(Fig. 29a). Rostrum rounded from immediately laterad of median carina to lateral margins, lateral margins rounded from above point of antennal insertion to anterior margin of eye. Dorsally lacking distinct large punctures. With small elongate-narrow appressed white, dense scales. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With sharp distinct median carina in anterior one-half. Subapical constriction slightly defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area broadly, shallowly to moderately deeply impressed. Dorsal punctures uniformly small, sparse and shallow, distance between punctures greater than diameter of one puncture (Fig. 29a). *Prosternum.* With shallow impression anterior to each procoxal cavity, and slightly developed transverse swelling anterior to each impression. *Elytra.* Moderately robust in general form (width at midlength 0.60-0.64 times length in male; 0.57-0.62 in female) (Fig. 22). In dorsal view with lateral margins straight and convergent from midlength to base, humerus obtuse, distinct (Fig. 22). All elytral intervals more or less uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed patches, one at basal one-third from intervals 2 to 6, the other at apical one-third from intervals 2 to 4 (Fig. 22). With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (equal to or greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small to moderately large, indistinct to distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-third of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from articles 1 and 2, present as elongate-oval pads on apical three-quarters of article 3; of mesotarsus of male, lacking from to as apical tuft of outer lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of female, lacking from articles 1 and 2, as small elongate-narrow pads on apical one-third of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical three-quarters of article 3; of metatarsus of female, lacking from articles 1 to 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (three examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms narrow, inwardly arcuate at midlength (Fig. 41). Male (seven examined). Abdominal sternum VIII with paired sclerite with inner apices truncate (Fig. 35c). Aedeagus elongate-narrow; in lateral view markedly arcuate, more so in basal one-half, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex asymmetrical, produced into rounded apical projection (Figs. 35a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with small dorsolaterally directed paired lobe on dorsal surface immediately beyond midlength; median dorsal pocket high, with large dorsolaterally directed paired lobe at basal one-third near ventral margin, separated from base of median pocket by trough (Fig. 47). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 47a).

Geographic distribution.— This species is known from widely scattered localities from Newfoundland west to Alberta (Fig. 205).

Chorological relationships.— This species is sympatric throughout the central and western part of its range with *S. parshus* and *S. immaculatus.* Individuals of these three species have been collected within a few days of each other at Fort McMurray, Alberta.

<div align="center">

Stephanocleonus stenothorax Anderson, new species

(Figs. 23, 30, 36, 42, 48, 204)

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Stephanocleonus plumbeus; Leng 1919 (in part; check., poss. misident.). Danks 1981 (in part; check., poss. misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "YT. Bluefish caves/ 67°08'N 140°48'W/ 2000' 4.vii.1983/R.J. Cannings", "HOLOTYPE/ *Stephanocleonus*/ *stenothorax*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Allotype, female, with a red label "ALLOTYPE", "YUKON: Dog. Ck./ 30.VII.77/ R.E. Roughley", "ALLOTYPE/ *Stephanocleonus*/ *stenothorax*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Bluefish Caves archaeological site, Yukon Territory.

Paratypes. 12 males, 11 females. Canada: Yukon Territory, Keele Range, Bluefish Caves archaeological site, 67°08'N 140°47'W, 1983, J. Cinq-Mars, 12M, 11F. (CNC, CWOB, JVM, RSAN, USNM, ZIL)

Derivation of specific epithet.— From the Greek "*stenos*" meaning narrowed, and "*thorax*" meaning breastplate. This name is used in reference to the apically narrowed form of the pronotum.

Problems in recognition.— Among North American species of *Stephanocleonus* with maculate elytra, individuals of this species are recognized by the pronotum with the lateral subapical constriction continued and well-defined dorsally, and with the apical margin

shallowly emarginate at the middle. The glabrous shiny tubercle at the confluence of elytral intervals 4 to 6 is markedly elevated and lateral arms of abdominal sternum VIII of the female are very broad and medially approximate to contiguous near their apices (Fig. 42). The shape of the aedeagus of the male is also distinctive (Figs. 36a,b).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 6. *Size.* Length, male, 12.5–13.1 mm; female, 12.8–14.9 mm. Width, male, 5.3–6.2 mm; female, 5.6–6.2 mm. *Head.* Frons with punctures large, moderately dense and deep, many punctures confluent in some specimens, surface thus longitudinally rugose; uniformly covered with small broad appressed white scales, dense laterally, sparse medially. Most specimens with slightly raised carina on vertex. *Rostrum.* Robust, (width at apex 0.90-0.95 times length in male; 0.90–1.00 in female) (Fig. 30). With well-developed, sharp, steeply declivous, low, median carina from above point of antennal insertion to base of rostrum; basally and apically terminated at small, shallow fovea (Fig. 30a). Rostrum flat from immediately laterad of median carina to lateral margins, lateral margins rounded to sharp from above point of antennal insertion to anterior margin of eye. Dorsally with punctures large moderately dense and deep, many confluent in some specimens, surface thus longitudinally rugose. With small elongate-narrow appressed white, scales; dense laterally, sparse medially. *Pronotum.* Dorsal apical margin broadly and moderately deeply emarginate at middle. With sharp distinct median carina in anterior one-half. Subapical constriction well defined laterally and dorsally; with distinct moderately deep impressions laterad of median carina continuous with lateral portion of subapical constriction. Median basal area broadly and moderately deeply impressed. Dorsal punctures small, sparse and shallow laterally and medially (except basally at middle where punctures are dense, deep, approximate and irregularly impressed), distance between punctures subequal to or greater than diameter of one puncture. *Prosternum.* With shallow impression anterior to each procoxal cavity, and with or without slightly to moderately developed transverse swelling anterior to each impression. *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.57-0.60 times length in male; 0.55-0.61 in female) (Fig. 23). In dorsal view with lateral margins straight and convergent from midlength to base, humerus obtuse, distinct (Fig. 23). All elytral intervals more or less uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, other at apical one-third from intervals 2 to 4 (Fig. 23). With markedly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (equal to or greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth moderately large, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-half of article 1, as large elongate-oval pads on apical two-thirds of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from articles 1 and 2, present as elongate-oval pads on apical one-half of article 3; of mesotarsus of male, lacking from to as apical tuft of outer lobe of article 1, as elongate-narrow pads on apical two-thirds of outer lobe and apical one-half on inner lobe of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of female, lacking from articles 1 and 2, as elongate-oval pad on apical one-half of outer lobe and as apical tuft of inner lobe of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical two-thirds of article 3; of metatarsus of female, lacking from articles 1 to 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms very broad, medially approximate or contiguous near apices, inwardly arcuate at midlength (Fig. 42). Male (four examined). Abdominal sternum VIII with paired sclerite with inner apices truncate (Fig. 36c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex not spatulate; in ventral view with apex symmetrical, medially rounded but not produced into distinct apical projection (Figs. 36a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with small dorsolaterally directed paired lobe on dorsal surface at midlength; median dorsal pocket moderately high, with moderately large dorsolaterally directed paired lobe at basal midline near dorsal margin (Fig. 48). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 48a).

Geographic distribution.— This species is known only from two localities in the northern Yukon Territory (Fig. 204).

Natural history.— Most specimens of the type series were collected in unbaited pitfall traps set in a partly forested limestone upland and fell-field. They were collected in association with *Lepidophorus lineaticollis* Kirby and *Vitavitus thulius* Kissinger and several species of dry-tundra Carabidae.

Chorological relationships.— This species is allopatric to all other *Stephanocleonus* species.

Genus *Apleurus* Chevrolat

Apleurus Chevrolat 1873:78. Gender, masculine. Type species *Apleurus fossus* Chevrolat (= *Cleonus lutulentus* LeConte) by subsequent designation (Casey 1891:186). Chevrolat 1873 (in part; catal., sp. desc.). Faust 1904 (key).

Notes about synonymy.— See "Notes about synonymy" section under subgenus *Apleurus*.

Diagnosis.— Adult Cleoninae with moderately elongate-narrow to very robust body form (Figs. 24, 68–80). Eye elongate teardrop shaped, slightly to moderately prominent and convex in dorsal view (Figs. 81–88). Rostrum with median carina lacking to variously developed (Figs. 84–86). Pronotum punctate, anterolateral margin of pronotum straight to with variously developed acute postocular projection; postocular vibrissae long, of unequal length and longest behind base of eye (Figs. 81–88). Disk with elongate white moderately large moderately dense scales present in lateral stripe of variable width, small and fine in moderately broad to very broad apically narrowed median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 24, 68–80). Antenna with funiculus with article 1 longer than, to more or less equal in length to, article 2; article 2 more or less as long as wide, to slightly longer than wide (Figs. 81–88). Ventral tarsal pilosity various but reduced to some extent (not extended over entire ventral surface of tarsal article) to lacking entirely from at least more basal tarsal articles (especially of metatarsus). Tibia with corbel ridge sharp (Fig. 6). Prosternum with swellings absent or present, if present, located immediately anterior to each prosternal impression (Fig. 7). Female with abdominal sternum VIII lacking basal arm (Figs. 89–96).

Description.— *Size.* Small to large, moderately elongate-narrow to very robust in body form. *Mouthparts.* Prementum flat to slightly swollen, lacking or with as many as five large setae on each side (Figs. 61–63). Maxillary palpus with palpifer with large seta, stipes with or without large seta (Figs. 64–65). Labial palpi separated by a distance varied from subequal to, to twice width of basal article of a labial palpus (Figs. 61–63). *Rostrum.* Moderately to markedly robust, not medially tumescent (Figs. 81–88). Median carina lacking to low, moderately rounded to sharp (Figs. 81–88). Epistoma not swollen, produced anteriorly, with apical margin emarginate (Fig. 81b) or rounded medially (Figs. 82b–88b). Antenna with funiculus with article 1 subequal in length to, to slightly longer than article 2 (Figs. 81a–88a); apical three articles of club with placoid sensillae. *Head.* Eye elongate teardrop shaped, slightly to moderately prominent and convex in dorsal view (Figs. 81–88). Area behind eye with moderately deep irregular punctures. Upper margin of eye rounded to sharp, frons convex to more or less flat. *Vestiture.* Dorsum with suberect or erect vestiture lacking to very long and dense; with simple elongate-narrow appressed white scales of variable size and density. *Prothorax.* Dorsal surface of pronotum punctate. Pronotum with median basal area shallowly to deeply impressed; anterolateral margin, behind eyes, straight to with variously developed acute postocular projection; postocular vibrissae long, of unequal length and longest behind base of eye (maximum length greater than or equal to one-half width of eye) (Figs. 81a–88a); disk with elongate white moderately large moderately dense scales present in lateral stripe of various width, small and fine in moderately broad to very broad apically narrowed median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 24, 68–80). Prosternum with slight to moderately deep impression anterolaterad of each procoxal cavity; with or without slight to markedly developed swelling immediately anterior to each prosternal impression (Fig. 7). *Legs.* Foretarsus moderately broad, articles 2 and 3 more or less subequal in length, at most only slightly longer than broad; article 1 only slightly longer than articles 2 or 3; article 3 moderately deeply bilobed. Meso- and especially metatarsus slightly more elongate-narrow, article 2 slightly to distinctly longer than article 3; article 1 distinctly longer than articles 2 or 3; article 3 moderately deeply bilobed. Ventral tarsal pilosity various but reduced to some extent (not covering entire ventral surface of a tarsal article) to lacking entirely from at least more basal tarsal articles (especially of metatarsus). Claws variously connate from near base to through basal one-third, slightly to markedly divergent. Foretibia with inner margin with at most only small denticles in apical one-half; near apex with second spur very slightly to moderately well-developed. Metatibia of male with ventral margin of uncus evenly rounded. Tibia with corbel ridge sharp (Fig. 6). *Wings.* Absent or present (various in length). *Elytra.* Intervals, except humerus and bases of intervals 3 and 5 flat, to with sutural interval and intervals 3, 5, 7, and 9 variously slightly to markedly swollen and convex. Striae distinctly punctate. Humeri acute to rounded. Scale pattern various (Figs. 24, 68–80). *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed scale to uniformly covered with fine dense hair-like scales. Abdominal sternum VII in males with apical margin at middle with or without small dorsally directed median tooth. Abdominal terga VII and VIII of female not, or slightly to markedly longitudinally carinate. *Genitalia.* Female. Abdominal sternum VIII lacking basal arm (Figs. 89a–96a).

Gonocoxite II elongate triangular in form, apex not prolonged into marked lobe; stylus absent or present, small to moderately large in size; apical to slightly anteapical in position (Figs. 89b–96b). Spermathecal gland round (Fig. 60). Male. Abdominal sternum VIII with interior angle of each sclerite lacking basal projection to with basal projection slightly to markedly developed (Figs. 97f, 101e, 103e). Aedeagus moderately robust, in lateral view more or less evenly arcuate throughout length; apex not spatulate (Figs. 97d, 98c–104c). Internal sac various; with dorsal median pocket low to high; apical and dorsal median pockets individually distinct; various lobes present, lobe A absent (Figs. 97a,b–104a,b). Apical sclerite complex with individual sclerites scythe-like (Figs. 97c, 98d–104d).

Comparisons.— Species of *Apleurus* are most likely to be confused with the Palearctic *Chromoderus* and the South African *Cnemodontus*. Members of these three genera either lack pronotal postocular lobes entirely or possess variously developed acute postocular projections. *Apleurus* species are separated from species of these other two genera by the ventral tarsal pilosity reduced in extent and also by characters in the male genitalia (see "Phylogenetic Analysis" section). Species of *Pleurocleonus* also lack a pronotal postocular lobe but are readily separated from *Apleurus* by the possession of a low broad longitudinally sulcate median rostral carina, flat eyes, and characters of male and female genitalia.

In the New World, some *Apleurus* species may be confused with large *Cleonidius* species which lack a pronotal postocular lobe. Consultation of diagnoses and key characters will readily separate the two.

Checklist of included species.— Eight species, assigned to two subgenera, are included in this endemic New World genus. These species are:

Subgenus *Gibbostethus* Anderson, new subgenus
       1. A.(G.) hystrix (Fall)
Subgenus *Apleurus* Chevrolat
       2. *A.(A.) aztecus* (Champion)
       3. *A.(A.) lutulentus* (LeConte)
       4. *A.(A.) porosus* (LeConte)
       5. *A.(A.) angularis* (LeConte)
       6. *A.(A.) jacobinus* (Casey)
       7. *A.(A.) albovestitus* (Casey)
       8. *A.(A.) saginatus* (Casey)

Phylogenetic relationships.— See "Phylogenetic analysis" section.

Subgenus *Gibbostethus* Anderson, new subgenus

Dinocleus; Fall 1913 (in part; sp. desc.). Leng 1920 (in part; catal.).
Cleonus (*Dinocleus*); Csiki 1934 (in part; catal.).
Cleonis; O'Brien and Wibmer 1982 (in part; catal., distn.).

Derivation of name.— Derived from the Greek "*gibbos*" meaning protuberant or swollen, and "*stethos*" meaning chest or breast. This name is used in reference to the tumescent mesosternal process of members of the single species placed in this subgenus.

Type species.— *Dinocleus hystrix* Fall by monotypy.

Diagnosis.— *Apleurus* with moderately elongate-narrow body form (Fig. 24). Dorsal erect vestiture dense and long. Prementum with bases of labial palpi separated by distance more or less equal to twice width of basal article of labial palpus (Fig. 61). Maxillary palpus with palpifer with large seta (Fig. 65). Rostrum with epistoma with apical margin emarginate medially (Fig. 81b). Mesosternum with mesosternal process markedly tumescent and convex (Fig. 58). Female with abdominal sternum VIII with lateral arms arcuate (Fig. 89a);

gonocoxite II with stylus moderately large, apical in position (Fig. 89b). Male with abdominal sternum VIII with each sclerite with rounded interior angles, basal projections lacking (Fig. 97f); aedeagus in dorsal view markedly laterally expanded from midlength to apical one-third (Fig. 97e).

Included species.— *Apleurus (Gibbostethus) hystrix* Fall from southern California is the only species in the subgenus.

Phylogenetic relationships.— This subgenus is sister to the remainder of *Apleurus*. Recognition as a distinct subgenus is warranted by the primitive phylogenetic position of the species and the sister-group relationship with the remainder of *Apleurus*, by a restricted and likely relictual distribution (Fig. 212), and by various autapotypic character states and character states exhibited by *Gibbostethus* which although interpreted as evolved independently, are homoplasious in derived *Apleurus* species (see "Phylogeny" section).

Apleurus (Gibbostethus) hystrix (Fall), new combination
(Figs. 24, 58, 61, 65, 81, 89, 97, 212)

Dinocleus hystrix Fall 1913:41. Holotype (examined), male, labelled "Pasadena/ Cal.", "Feb.", "Not in/ Lec.Coll.", "TYPE", "M.C.Z./ Type/ 25191", "H.C.FALL/ COLLECTION", "*Dinocleus/ hystrix/* Fall" (MCZC). Type locality, Pasadena, California. Leng 1920 (catal.).
Cleonus (Dinocleus) hystrix; Csiki 1934 (catal.).
Cleonis hystrix; O'Brien and Wibmer 1982 (catal., distn.).

Problems in recognition.— A distinctive and easily recognized species, *A. hystrix* is characterized by the markedly tumescent mesosternal process (Fig. 58) and the rostrum with the apical margin of the epistoma emarginate medially (Fig. 81b). The markedly laterally expanded aedeagus of males is also characteristic of this species (Fig. 97e).

Although it is unlikely that *A. hystrix* may be confused with other species of *Apleurus*, individuals may be confused with species of *Cleonidius* because of their small size and more elongate general body form (Fig. 24). Among other characters, *A. hystrix* individuals can be separated from *Cleonidius* individuals by the presence in the former of low rounded swellings on the prosternum immediately anterior to the prosternal impressions (Fig. 7). Swellings may or may not be present in *Cleonidius* species, but if present are situated immediately anterior to the procoxal cavities, adjacent to the prosternal impression (Fig. 8).

Description.— *Specimens examined.* 18 males, 11 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 7. *Size.* Length, male, 7.0–9.5 mm; female, 8.0–10.6 mm. Width, male, 2.8–3.5 mm; female, 3.0–4.2 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with dense, large, irregularly impressed, deep punctures. Frons also with dense, very long erect white hair-like scales. Area immediately behind posterior margin of eye with very large, deep, irregularly impressed punctures. Area above eyes slightly to moderately elevated above rest of frons (eyes apparently browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.69-0.85 times length in male; 0.70-0.82 in female) (Fig. 81). Median carina absent. Dorsal and lateral punctation dense, large, deep and irregularly impressed, some punctures longitudinally confluent medially. Dorsally, excluding epistoma, with dense, very long, erect white hair-like scales and dense very elongate-narrow recumbent white scales. In lateral view only slightly declivous from point of antennal insertion to apex (Fig. 81a). Epistoma with apical margin shallowly emarginate at middle (Fig. 81b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (Fig. 65). Labial palpi separated by more or less twice width of base of a labial palpus (Fig. 61). Prementum with one pair of large setae (Fig. 61). *Pronotum.* In dorsal view with lateral margins subparallel to slightly divergent from base to apical one-quarter; constricted at oblique angle anterior to apical one-quarter; apical one-quarter and base subequal in width to slightly wider at apical one-quarter; distinct lateral tubercles not evident (Fig. 24). Dorsal punctation large to very large, dense and deep; punctures sparser smaller and shallower laterally and on flanks. Scales white, elongate-narrow, recumbent, sparse and small or lacking medially from disk (except for midline and along apical margin), uniformly dense laterally, sparser at lateral margins and on flanks (Fig. 24). Median carina lacking. Dorsally covered throughout with dense very long erect white hair-like scales each situated within large puncture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 81a). *Prosternum.* With very shallow impression anterior to each

procoxal cavity and with moderately developed rounded swelling anterior to each prosternal impression (Fig. 81a). *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.53–0.66 times length in males; 0.54–0.64 in females) (Fig. 24). In dorsal view with lateral margins straight to very slightly arcuate from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex (Fig. 24). Humerus rounded, indistinct. Dorsally with dense, very long erect hair-like scales. Sutural interval, and intervals 3 and 5 very slightly elevated and convex, especially basally. Scales elongate-narrow, recumbent, white, uniformly moderately dense except absent to sparse small and fine on interval 4 at basal one-third and apical one-third (Fig. 24) *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, indistinct from tibial denticles. Foretibial, mesotibial and metatibial unci of both sexes large. Tarsal claws not to very slightly divergent, basal internal flange distinct. Ventral tarsal pilose vestiture of foretarsus of male and female present as small rounded apical pads of article 1, as small rounded pads on apical one-third of article 2 and apical one-half of article 3; of mesotarsus of male present as apical tufts to small rounded apical pads of article 1, as small rounded apical pads to small rounded pads on apical one-third of article 2 and apical one-third to one-half of article 3; of mesotarsus of female present as apical tufts of article 1, as small rounded apical pads of article 2, and as rounded pads on apical one-third of article 3; of metatarsus of male and female present as apical tufts of article 1, as small rounded apical pads of article 2, and as rounded pads covering apical one-third of article 3. *Mesosternum.* Mesosternal process markedly swollen and tumescent (Fig. 58). *Abdomen.* Ventral surface with moderately dense, elongate-fine recumbent white scales and short suberect white hair-like scales. Abdominal sterna lacking distinct glabrous patches. Apex of abdominal sternum VII of male lacking dorsally directed tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (two examined). Abdominal sternum VIII with lateral arms narrow, straight and divergent in basal one-half, moderately and evenly inwardly arcuate from midlength to apex (Fig. 89a). Gonocoxite II with stylusmoderately large, slightly anteapical in position (Fig. 89b). Male (two examined). Abdominal sternum VIII with paired sclerite with inner apices lacking ventral projections (Fig. 97f). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view markedly laterally expanded at approximately midlength (Figs. 97d,e). Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength and small laterally directed lobes near basal margin at basal one-third (Figs. 97a,b). Eversible apical sclerite complex with paired scythe-like sclerites only slightly sclerotized, each with small median projection (Fig. 97c); adjacent ventral surface and basal portion of sides of apex of internal sac unsclerotized (Fig. 97a).

Geographic distribution.— This species has the most restricted distribution of any species of *Apleurus*. It has been found only in southern California, primarily in Los Angeles County at the El Segundo sand dunes but also at Pasadena; a single specimen is from Palm Springs, Riverside County (Fig. 212).

Natural history.— This species appears to be restricted to sand dune habitats in the Pacific semi-desert region of southern California. Adults have been collected on *Chaenactis glabriuscula* DC., *Aplopappus ericoides* (Less.) H. & A. (Compositae); *Croton californicus* Muell.-Arg. (Euphorbiaceae); and, *Lupinus albifrons* Benth. (Leguminosae). Definite host plants have yet to be determined. Adults have been collected from February to July at elevations of from 33–313 m (N = 3) (Fig. 232).

Chorological relationships.— This species is sympatric with extreme western *A. angularis* and *A. albovestitus*, and southern *A. jacobinus*.

Phylogenetic relationships.— This species is the sister-group to the rest of *Apleurus* (Figs. 234 and 235).

Subgenus *Apleurus* Chevrolat

Cleonus; LeConte 1858 (sp. descs.). LeConte 1859 (sp. desc.). Gemminger and von Harold 1871 (in part; catal.). Leng 1920 (in part; catal.). Bradley 1930 (in part; key). Blackwelder 1947 (in part; check.). Arnett 1960–1962 (in part; key, catal.). Tanner 1966 (in part; sp. redesc., biol.). Krombein 1979 (in part).

Apleurus Chevrolat 1873:78. Gender, masculine. Type species *Apleurus fossus* Chevrolat (= *Cleonus lutulentus* LeConte) by subsequent designation (Casey 1891:186). Chevrolat 1873 (in part; catal., sp. desc.). Faust 1904 (key).

Centrocleonus LeConte 1876a:145 [not Chevrolat 1873:62]. NEW SYNONYMY Type species *Cleonus angularis* LeConte, according to article 67 (h) of the International Code of Zoological Nomenclature. Gender, masculine. Henshaw 1881–1882 (check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1889. Horn 1894 (check.).

Cleonopsis LeConte 1876a:147. NEW SYNONYMY Gender, feminine. Type species *Cleonus pulvereus* LeConte (= *Cleonus lutulentus* LeConte) by monotypy. LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1889.

Wickham 1896 (check.).
Cleonaspis LeConte 1876a:153. NEW SYNONYMY Gender, feminine. Type species *Cleonus lutulentus* LeConte by
monotypy. Henshaw 1881–1882 (check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1902
(check.).
Stephanocleonus; Henshaw 1881–1882 (in part; check.).
Dinocleus Casey 1891:176. NEW SYNONYMY. Gender, masculine. New name for *Centrocleonus* LeConte. Type
species *Cleonus angularis* LeConte by subsequent designation (Faust 1904:190, error as "Typus *angulatus* Lac",
subsequently listed, p. 274, as "*angularis* Lec"). Wickham 1896 (check.). Fall 1901 (check.). Wickham 1902 (check.).
Champion 1902–1906 (sp. desc., notes). Casey 1904 (sp. desc.). Faust 1904 (key). Fall and Cockerell 1907 (check.).
Leng 1920 (catal.). Bradley 1930 (key). Tanner 1934 (check.). Ting 1936 (morphol.). Bruhn 1947 (morphol.). Van
Dyke 1953 (sp. desc.). Essig 1958 (biol.). Sanders 1960 (morphol.). Arnett 1960–1962 (key, catal.). Hatch 1971
(key).
Cleonus (*Apleurus*); Casey 1891 (key). Champion 1902–1906 (sp. desc., redescs.). Fall and Cockerell 1907 (check.). Csiki
1934 (catal.).
Cleonurus Faust 1904:274. *Nomem nudum*, incorrectly attributed to LeConte 1876a:152.
Cleonus (*Dinocleus*); Csiki 1934 (catal.). Blackwelder 1939 (check.). Kissinger 1964 (check.).
Cleonus (*Cleonopsis*); Kissinger 1964 (check.).
Cleonis; O'Brien and Wibmer 1982 (in part; catal., distn.). O'Brien and Wibmer 1984 (in part).

Notes about synonymy.— The genus *Apleurus* was initially established by Chevrolat
(1873) to include three new Mexican and southwestern United States species, and one
previously described southwestern United States species. Three of these species, *A. boucardi*,
A. trivittatus and *A. quadrilineatus*, were regarded as "espèces lyxiformes" by Chevrolat
(1873:109) thereby indicating their similarity to members of the genus *Lixus* and focusing
attention on their lack of similarity to *A. fossus*, the fourth member of the genus.

No type species was designated by Chevrolat although he (1873:80) stated in his treatment
of *A. boucardi* that "le corps de cet insecte est plus ovalaire que chez le type". This suggests
that he considered as type one of the other two species (*Cleonidius trivittatus* was not treated in
detail but merely placed in *Apleurus* by Chevrolat). *Apleurus fossus* was subsequently clearly
designated as the type species by Casey (1891:76).

LeConte (1876a) undertook the first comprehensive revision of North American Cleoninae,
wherein he proposed three new genera; *Centrocleonus* (a junior homonym of *Centrocleonus*
Chevrolat), *Cleonopsis* and *Cleonaspis*. Species of *Centrocleonus* LeConte were characterized
by the supposed unique presence of prosternal spines in front of the procoxae. Both *Cleonopsis*
and *Cleonaspis* were monobasic genera distinguished from other Cleoninae, most notably
Cleonus, primarily on the basis of features of the tarsi and antennae. I find LeConte's proposal
of *Cleonopsis* and *Cleonaspis* puzzling for they are based on forms which I consider to be
conspecific, differing only slightly in the extent of ventral tarsal pilosity, but otherwise not to
the extent discussed by LeConte (1876a:144–145, in key) as characteristic (see also "Notes on
synonymy" of *A. lutulentus*). Apparently LeConte (1876a) was not concerned that these two
genera might be confused, for in his descriptions of each, only characters permitting separation
from *Cleonus* are discussed.

LeConte (1876a) assigned the "espèces lyxiformes" of Chevrolat (1873) to *Cleonus* along
with a number of newly described North American species which Casey (1891) subsequently
placed in his new subgenus *Cleonidius*. No mention is made of *A. fossus* by LeConte (1876a)
and it is likely that he did not see this species for it did not occur within the geographic area of
immediate concern to him.

In the next major work on North American species, Casey (1891) recognized that the
distribution of the character states considered diagnostic of *Apleurus* also necessitated
inclusion of the species of *Cleonopsis* and *Cleonaspis*, and that these latter two taxa did not
warrant separate generic group status. He did not, however, consider *Apleurus* as warranting
any more than subgeneric status under *Cleonus*. *Dinocleus*, proposed as a new name for

Centrocleonus LeConte, and considered as of generic rank, included all of LeConte's *Centrocleonus* as well as many new species.

My use of *Apleurus* is decidedly broader than that of any of these authors, including not only those species regarded as *Apleurus* by Casey (1891) but also all those placed in *Dinocleus* Casey (1891), all subsequently described *Dinocleus* species and lastly, *Cleonus aztecus* Champion. Support for this broader definition is seen in the reconstructed phylogeny of these species wherein species of *Dinocleus* are placed as no more than derived species of *Apleurus*. Recognition of *Dinocleus* as a distinct genus would make *Apleurus* paraphyletic, an undesirable result because *Apleurus* are insufficiently structurally or biologically distinct from *Dinocleus* to warrant recognition as a formal paraphyletic taxon. The broader definition of *Apleurus* employed herein was also indirectly suggested by Van Dyke (1953) in his description of *Dinocleus bryanti*. Because *D. bryanti* is clearly conspecific with forms then regarded by Casey (1891), and I suspect also by Van Dyke, as *Apleurus*, Van Dyke's placement of his new species suggests a broader definition of *Dinocleus* and implies recognition of the similarities of members of that genus to those previously assigned to *Apleurus* even though it is doubtful he examined representatives of the latter.

Diagnosis.— Adult *Apleurus* with moderately robust to very robust body form (Figs. 68–80). Dorsal suberect or erect vestiture absent to very long and dense. Prementum with labial palpi separated by distance subequal to width of basal article of labial palpus (Figs. 62–63). Maxillary palpus with palpifer and stipes each with large seta, or with only palpifer with large seta (Fig. 64). Rostrum with epistoma with apical margin rounded medially (Figs. 82b–88b). Mesosternum with mesosternal process flat to only slightly convex (Fig. 59). Female with abdominal sternum VIII with lateral arms straight or arcuate (Figs. 90a–96); gonocoxite II with stylus absent or present, small to moderately large, apical to anteapical in position (Figs. 90b–96b). Male with abdominal sternum VIII with each sclerite with basal projection at interior angle slightly to markedly developed (Figs. 101e, 103e). Aedeagus in dorsal view more or less uniform in width throughout median portion of length.

Included species.— Seven species are placed in the subgenus *Apleurus*. They are found in the southwestern United States of America south to southern Mexico.

Phylogenetic relationships.— This subgenus is the monophyletic sister-group of the subgenus *Gibbostethus* (see "Phylogeny" section).

Key to species of adult *Apleurus (Apleurus)*

1   Elytra with sutural interval, intervals 3, 5, 7, and 9 markedly elevated and
           convex throughout greater part of their lengths. Metathoracic wings absent 2
1′   Elytra with all intervals flat or with sutural interval, intervals 3, 5, and 7
           only very slightly elevated and convex. Metathoracic wings present,
           variable in length from short (approximately one-half length of elytra) to
           long (equal to or greater than elytra in length) 6
2   (1)   Prosternum lacking swelling or with at most low rounded swelling anterior
           to each prosternal impression (Fig. 82a). Rostrum lacking median carina.
           Elytra very robust (width at midlength greater than 0.70 times length)
           (Fig. 68) .... *A. aztecus* (Champion), p. 474
2′   Prosternum with prominent swelling anterior to each prosternal impression
           (Figs. 84a–88a). Rostrum with median carina (obscured in some specimens

by large deep punctures) (Figs. 84–86). Elytra less robust (width at midlength less than 0.75 times length) (Figs. 70–73) 3

3 (2′) Tarsal claws slender, widely divergent, each lacking basal internal flange, tapered evenly from base to apex (Fig. 66). Dorsal erect vestiture of pronotum and elytra short. 4

3′ Tarsal claws robust, not widely divergent, each with basal internal flange, tapered abruptly from midlength to apex (Fig. 67). Dorsal erect vestiture of pronotum and elytra short or long 5

4 (3) Abdomen ventrally with scales broad, moderately dense; at least sterna III and IV with distinct glabrus shiny patches, each with single long and erect hair . . . . *A. angularis* (LeConte) (in part), p. 481

4′ Abdomen ventrally with scales fine and elongate, extremely dense; no glabrous patches present . . . . *A. porosus* (LeConte) (in part), p. 478

5 (3′) Elytra with sutural interval, intervals 3, 5, 7, and 9 (especially 3 and 5 near base) markedly elevated and convex. Most specimens with dorsal vestiture of head, pronotum and elytra very long and erect and with rostrum with carina moderately well-developed (Fig. 86). Abdomen ventrally with scales fine and elongate, moderately dense; sterna III and IV with distinct glabrous shiny patches, each with single long and erect hair . . . .
. . . . *A. jacobinus* (Casey), p. 484

5′ Elytra with sutural interval, intervals 3, 5, 7, and 9 less markedly elevated and convex. Dorsal vestiture of head, pronotum and elytra short and suberect. Rostrum with carina only slightly developed, almost entirely obscured in some specimens by large deep punctures (Fig. 84). Abdomen ventrally with scales very fine and elongate, extremely dense; no glabrous patches present . . . . *A. porosus* (LeConte) (in part), p. 478

6 (1′) Pronotum laterally expanded immediately posterior to subapical constriction (giving distinctly tuberculate appearance); with base and apical one-quarter approximately equal in width to distinctly widest at apical one-quarter (Figs. 72–73). Tarsal claws slender, widely divergent, each lacking basal internal flange and tapered evenly from base to apex (Fig. 66) . . . .
. . . . *A. angularis* (LeConte) (in part), p. 481

6′ Pronotum not laterally expanded immediately posterior to subapical constriction (not appearing distinctly tuberculate); with base and apical one-quarter approximately equal in width to distinctly widest at base (Figs. 69, 74–80). Tarsal claws robust, not widely divergent; each with basal internal flange and tapered abruptly from midlength to apex (as in Fig. 67) 7

7 (6′) Tarsus of hind leg with venter of article 3 with large pubescent pad. Prosternum lacking swelling or with swelling anterior to each prosternal impression only slightly developed (Fig. 83a). Female with tergum VII not longitudinally carinate; gonocoxite II with stylus large (Fig. 91b) . . . .
. . . . *A. lutulentus* (LeConte), p. 475

7′ Tarsus of hind leg with venter of article 3 lacking large pubescent pad, with at most small apical tuft of pubescence. Prosternum with prominent swelling anterior to each prosternal impression (Figs. 87–88). Female with

tergum VII longitudinally carinate; gonocoxite II lacking stylus (Figs.
95–96) 8

8   (7′) Tarsus of fore- and middle leg with venter of article 3 with large pubescent
pad .... *A. saginatus* (Casey) (in part; males), p. 491

8′   Tarsus of fore- and middle leg with venter of article 3 lacking large
pubescent pad, with at most small apical tuft of pubescence 9

9   (8′) Pronotum with lateral margins with outer margins of large punctures
swollen, shiny and glabrous (appearing as small distinct tubercles).
Abdomen ventrally (especially sterna III and IV) with distinct large
glabrous patches, each with single short and suberect scale situated in the
center .... *A. saginatus* (Casey) (in part; females), p. 491

9′   Pronotum with lateral margins with outer margins of large punctures not
swollen, glabrous or shiny. Abdomen ventrally either lacking glabrous
patches and with scales extremely dense; with small glabrous patches; or,
with most scales abraded .... *A. albovestitus* (Casey), p. 486

Apleurus (Apleurus) aztecus (Champion), new combination
(Figs. 68, 82, 90, 98, 210)

Cleonus aztecus Champion 1902–1906:99. Lectotype (here designated), male, one of two syntypes, labelled "Type",
inverted "Sp. figured", "Refugio/ Durango/ Hoge.", "B.C.A. Col. IV.4./ *Cleonus/ aztecus,/* Champ." and with my
designation label "LECTOTYPE/ *Cleonus aztecus*/ Champ. desig./ Anderson" (BMNH). Type locality, Refugio,
Durango, Mexico.
Cleonis aztecus; O'Brien and Wibmer 1982 (catal., distn.).

Problems in recognition.— Members of this species are most likely to be confused with
brachypterous specimens of *A. lutulentus*. In these latter specimens, the alternate elytral
intervals are slightly elevated and convex and the elytra are moderately robust (more so than in
macropterous *A. lutulentus*). These individuals are sympatric with *A. aztecus* and although
superficially similar, *A. aztecus* individuals are distinguished by the tarsal claws each lacking a
basal internal flange (as in Fig. 66), lack of metathoracic wings, and lack of a dorsally directed
tooth on the apical margin of abdominal sternum VII in males.

A. aztecus individuals may also be confused with those other species of *Apleurus* in which
alternate elytral intervals are elevated and convex. Key characters should readily serve to
separate these species.

Description.— *Specimens examined.* 16 males, 7 females. Data about variation in LR, WF, WRA, LP, WPB,
WPT, WEIM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 8.
Size. Length, male, 5.6–9.4 mm; female, 5.2–9.4 mm. Width, male, 2.9–4.6 mm; female, 2.5–4.8 mm. *Head.* Eye
prominent and convex in dorsal view. Frons and vertex with moderately dense, small to moderately large, deep punctures.
Frons also with sparse, short suberect white hair-like scales immediately above eyes. Area immediately behind posterior
margin of eye with large, deep, irregularly impressed punctures. Area above eyes slightly elevated above rest of frons (eyes
apparently browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Robust (width at
apex 0.79–1.00 times length in male; 0.78–0.91 in female) (Fig. 82). Median carina absent. Dorsal and lateral punctation
moderately dense, small to large, deep. Dorsally, excluding epistoma, with moderately dense, short, suberect white
hair-like scales and moderately dense elongate-narrow appressed white scales. In lateral view with apical portion flat to
only very slightly declivous from point of antennal insertion to apex (Fig. 82a). Epistoma with apical margin rounded at
middle (Fig. 82b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial
palpi separated by more or less width of basal article of labial palpus (as in Fig. 62–63). Prementum with one pair of large
setae (as in Fig. 62). *Pronotum.* In dorsal view with lateral margins subparallel to slightly divergent from base to apical
one-quarter; constricted at oblique angle anterior to apical one-quarter; apical one-quarter and base subequal in width to
slightly wider at apical one-quarter; without distinct lateral tubercles (Fig. 68). Dorsal and lateral punctation small, sparse
to moderately dense and shallow; punctures sparser and smaller on flanks. Scales white, elongate-narrow, appressed, sparse
and small or lacking medially from disk and dorsally from flanks (except for midline and area anterior to low transverse

carina if present), dense laterally to lateral margins in anterior two-thirds and ventrally on flanks. Median carina lacking; some specimens with low median transverse carina or impunctate area at midlength. Dorsally with dense very short fine suberect white hair-like scales each situated within large puncture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 82a). *Prosternum.* With very shallow impression anterior to each procoxal cavity and with at most a low slightly developed rounded swelling anterior to each prosternal impression (Fig. 82a). *Elytra.* Very robust in general form (width at midlength 0.70–0.90 times length in males; 0.72–0.80 in females) (Fig. 68). In dorsal view with lateral margins moderately arcuate throughout length (Fig. 68). Humerus rounded, indistinct. Dorsally with sutural interval and intervals 3, 5, 7, and 9 with multiple rows of short fine suberect hair-like scales; intervals 2, 4, 6, and 8 with only single row of similar hair-like scales. Sutural interval, and intervals 3, 5, 7, and 9 markedly elevated and convex throughout their lengths. Scales various in density and size; elongate-narrow, pattern various but with at least small glabrous (or nearly so) area immediately apicad of midlength on interval 4 (Fig. 68). *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth large, distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes small. Tarsal claws widely divergent, no basal internal flange present (as in Fig. 66). Ventral tarsal pilose vestiture of foretarsus of male present as small rounded apical pads of article 1, as elongate-oval pads on apical one-half of article 2, and as large elongate-oval pads covering apical two-thirds of article 3; of foretarsus of female present as small rounded apical pads on articles 1 and 2, as rounded pads on apical one-third to one-half of article 3; of mesotarsus of male present as minute apical tufts on articles 1 and 2, and as small rounded apical pads to small rounded pads on apical one-half of article 3; of mesotarsus of female absent to present as minute apical tufts on articles 1 and 2, and as small rounded apical pads of article 3; of metatarsus of male present as minute apical tufts on articles 1 and 2, and as minute to small apical tufts of article 3; of metatarsus of female absent on articles 1 and 2, and present as minute apical tuft of article 3. *Mesosternum.* Mesosternal process moderately convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with moderately dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with moderately dense, small, individually indistinct to distinct rounded glabrous shiny patches, each with large puncture and single long erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male lacking dorsally directed tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (two examined). Abdominal sternum VIII with lateral arms narrow, very slightly sinuate and markedly inwardly arcuate near apex (Fig. 90a). Gonocoxite II with stylus moderately large, slightly anteapical in position (Fig. 90b). Male (three examined). Abdominal sternum VIII with paired sclerite with inner apices lacking or with only slightly developed ventral projections. Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel sided throughout length. Internal sac elongate and low, only slightly apically deflexed; median dorsal pocket low, with moderately large dorsolaterally directed paramedial lobe at midheight at basal one-third, small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket, and moderately large dorsolaterally directed paramedial lobes at midheight at apical one-third (Figs. 98a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites well sclerotized, each lacking median projection (Fig. 98d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of well-developed transverse sclerites (Fig. 98a).

Geographic distribution.— This species is found throughout the highlands of central México (Fig. 210).

Natural history.— This species appears to be restricted to the xeric high-elevation mesquite-grasslands of central México (pastizal and perhaps pastizal-matorral xerofilo transition of Rzedowski [1978]). Adults have been collected on *Solidago* sp. (Compositae). Other adults have been collected from under prickly-pear pads, stones and dry cow dung. Definite host plants are unknown. Adults have been collected from June to August at elevations from 2250–3385 m (N=8) (Fig. 232).

Chorological relationships.— This species is sympatric throughout its range with *A. lutulentus*. Adult specimens of the two species have been collected together at 1.5 mi. S. Fresnillo (Zacatecas) and 20 mi. NE. Dolores Hidalgo (Guanajuato).

Phylogenetic relationships.— This species is the sister-species of the rest of the species in the subgenus *Apleurus* (Figs. 234–235).

Apleurus (Apleurus) lutulentus (LeConte), new combination
(Figs. 6, 59, 62, 69, 83, 91, 99, 207)

Cleonus lutulentus LeConte 1859a:18. Lectotype (here designated), female, one of two syntypes (only one examined), labelled with a dark green circle (=New Mexico), "Type/ 5186", "*Cleonaspis/ lutulentus/* (Lec)" and with my designation label "*Cleonus/ lutulentus/* LeC. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Santa Fe, New Mexico. Gemminger and von Harold 1871 (catal.). Leng 1920 (catal.).

Cleonus pulvereus LeConte 1859a:18. NEW SYNONYMY Holotype (examined), female, labelled "Dallas/ Tex/ Boll",
    "Type/ 5185", "*Cleonopsis/ pulvereus/* (Lec)" (MCZC). Type locality, Dallas, Texas. Gemminger and von Harold
    1871 (catal.). Leng 1920 (catal., error as *Cleonus pluvereus*). Blackwelder 1947 (check.). Krombein 1979 (as prey).
Apleurus fossus Chevrolat 1873:78. NEW SYNONYMY Lectotype (here designated), female, one of two syntypes,
    labelled "12....", "Mexico/ Au. Salle", "TYPUS", "40", "473/ 85", "Riksmuseum/ Stockholm" and with my
    designation label "*Apleurus fossus*/ Chevrolat/ LECTOTYPE/ desig. Anderson" (Riksmuseum, Stockholm; other
    syntype in BMNH). Type locality, Mexico. Faust 1904.
Cleonaspis lutulentus; LeConte 1876a (redesc.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902
    (check.).
Cleonopsis pulvereus; LeConte 1876a (redesc.). Henshaw 1885 (check.). Wickham 1889. Wickham 1896 (check.).
Stephanocleonus pulvereus; Henshaw 1881–1882 (check.).
Cleonus (Apleurus) fossus; Casey 1891 (designation as type species of *Apleurus* Chevrolat). Champion 1902–1906 (syn.,
    distn.). Csiki 1934 (catal.).
Cleonus (Apleurus) lutulentus; Casey 1891 (key). Fall and Cockerell 1907 (check.). Csiki 1934 (catal.).
Cleonus (Apleurus) pulvereus; Casey 1891 (key). Champion 1902–1906 (syn., distn.). Fall and Cockerell 1907 (check.).
    Csiki 1934 (catal.).
Cleonus fossus; Blackwelder 1947 (check.).
Dinocleus bryanti Van Dyke 1953:101. NEW SYNONYMY Holotype (examined), male, labelled "Seligman,/ Ariz. VIII
    3 36/ Bryant.112.", "From the/ O. Bryant/ Collection", "Holotype" (CASC). Type locality, Seligman, Arizona.
Cleonis bryanti; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis fossus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis lutulentus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis pulvereus; O'Brien and Wibmer 1982 (catal., distn.).
lutatentus, incertae sedis; Chevrolat 1873 (error, misspelling).
pulverosus, incertae sedis; Chevrolat 1873 (error, misspelling).

Notes about synonymy.— I can find no consistent differences that warrant separation of
Cleonus pulvereus LeConte, *Cleonus lutulentus* LeConte and *Dinocleus bryanti* Van Dyke as
distinct species. LeConte (1859a) emphasized characters (extent of ventral tarsal vestiture and
degree of development of rostral carina) which are intraspecifically variable in describing *C.
pulvereus* and *C. lutulentus* and subsequently placing them in separate genera (LeConte,
1876a) (see "Notes about synonymy" section for *Apleurus*). I have not seen any specimens of
A. lutulentus from which the ventral tarsal pilose vestiture is entirely lacking and in which the
tarsal articles are not bilobed, as was given by LeConte (1876a) as in part characteristic of *C.
lutulentus*, and I do not find that the characters subsequently given by Casey (1891) to
separate the two species represent anything more than intraspecific variation.

   Dinocleus bryanti Van Dyke is clearly *A. lutulentus*. Van Dyke (1953) considered *D.
bryanti* a member of the genus *Dinocleus*, however, since he did not mention either *Cleonus
pulvereus* or *Cleonus lutulentus*, and since neither was then considered to be *Dinocleus*, I
suspect that Van Dyke did not look at representatives of these forms in describing *D. bryanti*,
but only at those forms already placed in *Dinocleus*. As a result, he found his new species to be
very distinct from those then included in *Dinocleus*. As discussed elsewhere ("Notes about
synonymy" section for *Apleurus*) this placement of *D. bryanti* in *Dinocleus* concurs with my
classification of species of *Dinocleus* and *Apleurus* (including *Cleonaspis* and *Cleonopsis*)
herein as congeneric.

   I also consider the Mexican brachypterous *A. fossus* as conspecific with the other forms
discussed previously in this section. No specific type locality was given for this species but
because brachypterous individuals are otherwise only known from central and southern México
I suspect this is the area of collection of the type series. These brachypterous forms are
otherwise distinguished from typical *C. lutulentus* by a more robust and globose elytral form,
possession of elytral intervals 3, 5 and 7 slightly elevated and convex, and possession of deep
and large punctures on the head, pronotum and elytra. Although only this brachypterous form
occurs in the southern Mexican highlands of Oaxaca and Puebla, some of these similarly
brachypterous individuals are also known to be sympatric with typically macropterous

individuals in central México. Because wing length polymorphism and associated variation in elytral form is found in sympatric individuals of other species of *Apleurus* (*A. angularis* and *A. albovestitus*), I concur with Champion (1902–1906:98) that *A. fossus* is "probably nothing more than a southern form of *C. pulvereus* LeC.".

Problems in recognition.— Brachypterous specimens of this species may be confused with individuals of *A. aztecus* as noted in the "Problems in recognition" section for that species. They may also be confused with small *A. saginatus* or *A. albovestitus*, or macropterous *A. angularis*, but the presence of distinct prosternal swellings anterior to the prosternal impressions in members of the latter three species (Figs. 85, 87–88), among other key characters, will readily separate them from *A. lutulentus*.

Description.— *Specimens examined*. 334 males, 369 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 9. *Size*. Length, male, 5.3–10.3 mm; female, 6.4–11.4 mm. Width, male, 2.4–4.8 mm; female, 2.9–5.5 mm. *Head*. Eye prominent and convex in dorsal view. Frons and vertex with moderately dense, small to large, deep punctures. Frons lacking suberect or erect vestiture; with only sparse elongate-narrow appressed white scales. Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes flat, not distinct from rest of frons (eyes not appearing distinctly browed in anterior view). Width of frons greater than to subequal to width at apex of rostrum. *Rostrum*. Moderately robust (width at apex 0.65-0.91 times length in male; 0.67-0.84 in female) (Fig. 83). Median carina absent or at most only slightly developed and indistinct. Dorsal and lateral punctation moderately dense, small to large, deep; sparser apically and irregularly impressed medially in some specimens). Dorsally, excluding epistoma, with scattered very short, fine, suberect hair-like scales towards apex, and sparse elongate-narrow appressed white scales. In lateral view with apical portion flat to only very slightly declivous from point of antennal in ertion to apex (Fig. 83a). Epistoma with apical margin rounded at middle (Fig. 83b). *Mouthparts*. Maxillary palpus with stipes with large seta on outer margin (as in Fig. 64). Labial palpi separated by more or less width of basal article of a labial palpus (Fig. 62). Prementum with one pair of large setae (Fig. 62). *Pronotum*. In dorsal view with lateral margins slightly arcuate from base to apical one-quarter; constricted at oblique angle anterior to apical one-quarter; pronotum widest at base to subequal in width at base and at apical one-quarter; distinct lateral tubercles not evident (Fig. 69). Dorsal and lateral punctation small to large, moderately dense to dense, and deep; punctures sparser and smaller on flanks. Scales white, elongate-narrow, appressed, sparse and small or lacking medially from disk in a broad, apically narrowed patch (except for midline in some specimens), and at lateral margins near base; uniformly dense laterally to lateral margins in anterior one-half and ventrally on flanks. Median carina lacking. Dorsally lacking suberect or erect vestiture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 83a). *Prosternum*. With very shallow impression anterior to each procoxal cavity and with at most low slightly developed rounded swelling anterior to each prosternal impression (Fig. 83a). *Elytra*. Moderately robust in general form (width at midlength 0.57-0.72 times length in males; 0.52–0.76 in females) (Fig. 69). In dorsal view with lateral margins slightly arcuate and convergent to subparallel from apical one-third to humerus; markedly arcuate from apical one-third to apex; humerus obtuse to acute, moderately distinct to distinct (Fig. 69). Dorsal suberect or erect vestiture absent or at most with sutural interval and intervals 2 and 3 with very short suberect hair-like scales. Dorsally with all elytral intervals flat to slightly convex, to with sutural interval and intervals 3, 5, and 7 slightly swollen and convex in brachypterous individuals. Scales various in density and size; elongate-narrow, pattern various with numerous irregularly distributed small glabrous or nearly so areas (Fig. 69). *Wings*. Short (very slightly shorter than elytra in length [2.1%, N=15]) to long (greater than elytra in length [97.9%, N=688]). Branches of 2A not joined at base. *Legs*. Foretibia of female with inner margin with small to moderately large denticles throughout most of length; subapical tooth moderately large, distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes moderately large. Tarsal claws not divergent, with well-developed basal internal flange present. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate apical pads of article 1, as elongate-oval pads on apical one-half of article 2, and as large elongate-oval pads on apical two-thirds of article 3; of foretarsus of female present as small elongate apical pads of article 1, as moderately large elongate-oval pads on apical one-half of article 2, and as large elongate-oval pads on apical one-half to two-thirds of article 3; of mesotarsus of male present as elongate-narrow pads on apical one-third of article 1 and apical one-half of article 2, and as large elongate-oval pads on apical one-half to two-thirds of article 3; of mesotarsus of female present as elongate-narrow pads on apical one-third of article 1, as elongate-oval pads on apical one-half of article 2, and as large rounded pads on apical one-half of article 3; of metatarsus of male absent at article 1, present as elongate very narrow pads of article 2, and as elongate-oval pads on apical one-half of article 3; of metatarsus of female absent to as small elongate-narrow pads on apical one-quarter of article 1, as elongate very narrow pads on apical one-third of article 2, and as large rounded pads on apical one-half to two-thirds of article 3. *Mesosternum*. Mesosternal process flat to very slightly convex but not tumescent (Fig 59). *Abdomen*. Ventral surface with dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with sparse to moderately dense, small, individually indistinct to distinct rounded glabrous shiny patches, each with large puncture and single short erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male

with large dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (three examined). Abdominal sternum VIII with lateral arms narrow, very slightly inwardly arcuate in basal three-quarters, then markedly inwardly arcuate to apex (Fig. 91a). Gonocoxite II with stylus moderately large, anteapical in position by more or less length of stylus (Fig. 91b). Male (12 examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections. Aedeagus elongate-narrow, in lateral view subequal in thickness from base to midlength (Fig. 99c); in ventral view more or less parallel sided throughout length. Internal sac elongate and low, only slightly apically deflexed; median dorsal pocket low, with moderately large dorsolaterally directed paramedial lobe at midheight at basal one-third and small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 99a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites well sclerotized, each with short median projection (Fig. 99d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of well-developed transverse sclerites (Fig. 99a).

Geographic variation.— Some specimens from central México have larger and deeper punctures of the head, pronotum and elytra; more robust and globose elytra; elytral intervals 3, 5, and 7 slightly elevated and convex; and short wings. Only specimens with extreme states in all of these characters are found in the area of the southern border of the species range in the Mexican states of Oaxaca and Puebla.

Geographic distribution.— This species is found from Kansas, Oklahoma and eastern Texas, west to Arizona, disjunct to central and southern México (Fig. 207). The species does not appear to be found in the Chihuahuan desert region in México. There is a single questionable record from northeastern California.

Natural history.— This is the most widely distributed species of *Apleurus*. It is found in mesquite-grassland, grassland, and desert-grassland transitional habitats in México and the United States, and in the grassland-deciduous forest transitional zone. Adults have been collected in dry upland desert washes and grasslands on a wide variety of plants, but mostly Compositae, as follows: *Gossypium hirsutum* L. (cotton, Malvaceae); *Chenopodium* sp. (Chenopodiaceae); *Asclepias* sp., *A. subverticillata* (Gray) Vail (Asclepiadaceae); *Koeberlinia spinosa* Zucc. (Capparaceae); *Acacia* sp. (Leguminosae); *Baccharis* sp., *B. glutinosa* Pers., *Baileya pleniradiata* Harv. and Gray, *Chrysothamnus nauseosus* (Pall.) Britton,, *Flourensia cernua* DC., *Gutierrezia* sp., *Solidago* sp., *Verbesina enceloides* (Cav.) Benth. and Hook., *V. oreophila* Woot. and Standl., *Xanthium* sp. (all Compositae). Definite host plants are not known. Adults have been collected from March to October at elevations from 9–3058 m (N=77) (Fig. 232).

Chorological relationships.— This species is sympatric with *A. saginatus* in southern Arizona and New Mexico; with *A. aztecus* in central México; with *A. angularis* in New Mexico, western Texas, Colorado, western Oklahoma, and Arizona; and with *A. albovestitus* in Arizona, New Mexico, and western Texas.

Adults of *A. lutulentus* and *A. albovestitus* have been caught together near Portal, Arizona, on *Chrysothamnus nauseosus*. Adult specimens of *A. lutulentus* and *A. aztecus* have been collected together 1.5 mi. S. Fresnillo (Zacatecas), on *Solidago* sp., and 20 mi. NE. Dolores Hidalgo (Guanajuato).

Phylogenetic relationships.— This species is the sister-species of the *A. porosus-A. angularis-A. jacobinus-A. saginatus-A. albovestitus* lineage of *Apleurus* (Figs. 234–235).

Apleurus (Apleurus) porosus (LeConte), new combination
(Figs. 70, 84, 92, 102, 210)

Centrocleonus porosus LeConte 1876a:146. Holotype (examined), female, labelled with a silver circle with portion cut away (=Baja California) "Type/ 5239", "*C. porosus*/ Lec" (MCZC). Type locality, Cape San Lucas, Baja California Sur, Mexico. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Horn 1894 (check.).
Dinocleus farctus Casey 1891:181. NEW SYNONYMY Holotype (examined), male, labelled "Cal", "CASEY/ bequest/

1925", "TYPE USNM/ 37271", "*D./farctus/* Cas." (USNM). Type locality, California, near the southern border. Fall 1901 (check.). Leng 1920 (catal.).

Dinocleus porosus; Casey 1891 (key, redesc.). Leng 1920 (catal.).
Cleonus (Dinocleus) farctus; Csiki 1934 (catal.).
Cleonus (Dinocleus) porosus; Csiki 1934 (catal.).
Cleonus porosus; Blackwelder 1947 (check.).
Cleonus farctus; Hardy and Andrews 1976 (distn., prob. misident. *A. angularis*).
Cleonis farctus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis porosus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Both LeConte (1876a) and Casey (1891) based their species descriptions of *Centrocleonus porosus* and *Dinocleus farctus* on unique specimens. Having examined larger numbers of individuals from various localities, I conclude that the two are conspecific and the differences noted by Casey (1891) as species-specific are due to intraspecific variation or secondary sexual characteristics (the holotype of *C. porosus* is a female; that of *D. farctus*, a male).

The type locality of *D. farctus* is given by Casey (1891) as California, near the southern border. I have not seen any other *A. porosus* from the state of California.

Problems in recognition.— Members of this species are likely to be confused with *A. angularis* but can be distinguished from individuals of that species by the robust form of the tarsal claws, each possessing a basal internal flange in most specimens (as in Fig. 67); by the lack of distinct glabrous patches on the abdominal sterna; and by presence of only very short suberect dorsal vestiture in the former. Some specimens of *A. porosus* from various localities however, possess tarsal claws, which although moderately robust, lack a distinct internal flange.

Apleurus porosus specimens are also likely to be confused with *A. jacobinus* individuals particularly in Baja California Norte (and possibly also in southern California) where the species appear to be narrowly sympatric. *Apleurus jacobinus* specimens are distinguished from those of *A. porosus* by the long dorsal erect vestiture; alternate elytral intervals markedly elevated and convex; and abdominal sterna with distinct glabrous patches in the former. However, in the southern part of the range of *A. jacobinus* in Baja California Norte, individuals I examined have shorter dorsal erect vestiture and less markedly elévated elytral intervals than elsewhere throughout the species range, thus, approaching the states in *A. porosus* in these characters. Although the differences in degree of elevation of the elytral intervals and length of dorsal vestiture in these individuals should still allow for separation of *A. jacobinus* and *A. porosus*, the presence of distinct glabrous patches on the abdominal sterna of the former will allow for unequivocal separation of the two species. *Apleurus porosus* specimens also have the pronotum with scales uniformly very dense laterally and on the flanks, more or less obscuring the individual large punctures.

Many *A. porosus* can also be separated from *A. jacobinus* and *A. angularis* by their larger size, more elongate-narrow rostrum, and by the pronotum being widest at the base (see Figs. 105–106, 109).

Description.— *Specimens examined.* 23 males, 32 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WElM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 10. *Size.* Length, male, 5.8–13.6 mm; female, 6.9–15.2 mm. Width, male, 2.6–6.1 mm; female, 3.0–7.2 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with dense, large to very large, deep punctures. Frons and area immediately above eyes with sparse to moderately dense short suberect hair-like scales. Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes slightly elevated above rest of frons (eyes appearing distinctly browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately elongate-narrow (width at apex 0.61–0.68 times length in male; 0.62–0.69 in female) (Fig. 84). Median carina absent to slightly developed but distinct, almost entirely obscured in some specimens by large deep punctures. Dorsal and lateral punctation moderately dense, large, deep. Dorsally, excluding epistoma, with scattered short, fine, suberect hair-like scales towards apex, and dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from

point of antennal insertion to apex (Fig. 84a). Epistoma with apical margin rounded at middle (Fig. 84b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of a labial palpus (as in Figs. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins subparallel to slightly convergent from base to apical one-quarter; constricted at acute angle anterior to apical one-quarter; widest at base to subequal in width at base and apical one-quarter; distinct lateral tubercles evident (Fig. 70). Dorsal and lateral punctation large, moderately deep to deep, dense; punctures sparser and smaller on flanks. Scales white, elongate-narrow, appressed, sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in some specimens); uniformly dense laterally, at lateral margins and ventrally on flanks, more or less obscuring large punctures. Median carina lacking. Dorsally covered throughout with sparse, fine, short, erect hair-like scales. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 84a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 84a). *Elytra.* Moderately robust in general form (width at midlength 0.65-0.70 times length in males; 0.65-0.73 in females) (Fig. 70). In dorsal view with lateral margins moderately arcuate throughout length; humerus rounded, not distinct (Fig. 70). Sutural interval and intervals 3, 5, 7, and 9 with sparse, very short, suberect hair-like scales. Dorsally with sutural interval and intervals 3, 5, 7, and 9 slightly swollen and convex (more so basally in some specimens). Scales elongate-narrow, various in density and size; pattern various but in most specimens with two extensive glabrous (or nearly so) areas, one from area behind humerus, posteromedially directed to sutural interval at midlength, other continous with the former at midlength and directed laterally from sutural interval to interval 9; some specimens also with glabrous (or nearly so) area of variable extent at confluence of intervals 4 to 7 (Fig. 70). *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes moderately large. Tarsal claws not divergent, basal internal flange absent to present, well-developed. Ventral tarsal pilose vestiture of foretarsus of male absent of article 1, present as minute apical tufts of article 2, as moderately large rounded pads on apical one-third to one-half of article 3; of foretarsus of female, mesotarsus of male and female, and metatarsus of male lacking from articles 1 and 2, present as small rounded pads at apex of article 3; of metatarsus of female lacking from articles 1 and 2, present as minute pads at apex of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with very dense, elongate-fine appressed white scales and scattered suberect hair-like scales. Abdominal sterna lacking distinct glabrous patches, with at most only lateral margins of abdominal sterna III and IV with very small indistinct glabrous patches. Apex of abdominal sternum VII of male with small dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (four examined). Abdominal sternum VIII with lateral arms narrow, slightly outwardly arcuate in basal one-half, then parallel to near apex, markedly inwardly arcuate immediately before apex (Fig. 92a). Gonocoxite II with stylus very small, anteapical in position by more or less one-half length of stylus (Fig. 92b). Male (five examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections (as in Fig. 101e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel sided throughout length. Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 102a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites lightly sclerotized, each lacking median projection (as in Figs. 100d-101d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 102a).

Geographic variation.— None noted, but this may be due to the small number of specimens examined, especially from Baja California Norte where this species is at most narrowly sympatric with *A. angularis* and *A. jacobinus.*

Geographic distribution.— This species is found throughout Baja California Sud and Baja California Norte, México (Fig. 210). It may occur in the extreme south of California.

Natural history.— Label data indicate that most adults have been caught in sand dune areas in the "matorral xerofilo" of Baja California (Sonoran desert) and Pacific semi-desert region at elevations of from 6–144 m (N=5) (Fig. 232). Sleeper (pers. comm.) has collected numerous specimens from a woody *Encelia* species and a single specimen from *Encelia laciniata* Vasey and Rose (Compositae). Definite host plants are not known.

Chorological relationships.— This species has one of the more restricted distributions of *Apleurus* species. It is sympatric with extreme southern *A. albovestitus*, and at most narrowly sympatric to parapatric with its close relatives *A. angularis* and *A. jacobinus.*

Phylogenetic relationships.— *Apleurus porosus* is the sister-species of the *A. angularis-A. jacobinus* sister-species pair (Fig. 235). Presence of the apotypic state of tarsal claws each lacking a basal internal flange in some *A. porosus* and in *A. angularis* (Fig. 66) is either a

result of hybridization or of homoplasy, more likely the former.

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Apleurus (Apleurus) angularis (LeConte), new combination
(Figs. 66, 72–74, 85, 93, 100, 211)

</div>

Cleonus angularis LeConte 1859a:18. Lectotype (here designated), male, one of two syntypes (only one examined), labelled with a pale green circle (= Wyoming Territory) "*C. angularis*/ Beckwith Lec.", "Type/ 5182" and with my designation label "*Cleonus*/ *angularis*/ LeC. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Kansas. LeConte 1858 (*nomen nudum*). Gemminger and von Harold 1871 (catal.). Hatch 1971.

Centrocleonus angularis; LeConte 1876a (key, diag.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889.

Dinocleus denticollis Casey 1891:180. NEW SYNONYMY. Lectotype (here designated), female, one of five syntypes, labelled "Ari", "CASEY/ bequest/ 1925", "TYPE USNM/ 37269", "*D./ denticollis*/ Cas." and with my designation label "*Dinocleus*/ *denticollis*/ Csy. LECTOTYPE/ desig. Anderson" (USNM). Type locality, Peach Springs, Arizona. Wickham 1896 (check.). Casey 1904. Van Dyke 1953. Hatch 1971 (redesc.).

Dinocleus angularis; Casey 1891 (key, redescr.). Wickham 1902 (check.). Faust 1904 (desig. as type species of *Apleurus* Chevrolat; error as "*angulatus* Lac").

Dinocleus porcatus Casey 1904:321. NEW SYNONYMY Lectotype (here designated), female, one of two syntypes, labelled "Ogden/ Ut. Solt", "CASEY/ BEQUEST/ 1925", "TYPE USNM/ 37270", "*porcatus*" and with my designation label "*Dinocleus*/ *porcatus*/ Csy. LECTOTYPE/ desig. Anderson" (USNM). Type locality, Ogden, Utah. Fall and Cockerell 1907 (check.). Leng 1920 (catal.).

Cleonus denticollis; Leng 1920 (catal.). Tanner 1966 (biol.).

Cleonus (Dinocleus) angularis; Csiki 1934 (catal.).

Cleonus (Dinocleus) denticollis; Csiki 1934 (catal.).

Cleonus (Dinocleus) porcatus; Csiki 1934 (catal.).

Cleonus farctus; Hardy and Andrews 1976 (distn., prob. misident.).

Cleonis angularis; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis denticollis; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis porcatus; O'Brien and Wibmer 1982 (catal., distn.).

angularis, incertae sedis; Chevrolat 1873.

Notes about synonymy.— Geographic patterns of variation in states of structural features considered characteristic of *Cleonus angularis* LeConte, *Dinocleus denticollis* Casey, and *Dinocleus porcatus* Casey, suggest that only a single species warrants recognition and that these three names be placed in synonymy (see "Geographic variation" section).

I have only been able to locate and examine one of the two syntypes of *Cleonus angularis* LeConte.

Problems in recognition.— *Apleurus angularis* and *A. aztecus* are the only two species of *Apleurus* in which all individuals have the tarsal claws widely divergent and each lacking a basal internal flange (Fig. 66). This character state should serve to separate nearly all *A. angularis* from *A. jacobinus* and *A. porosus*. Most *A. angularis* can further be separated from most *A. jacobinus* by the presence of long dorsal erect vestiture and markedly elevated alternate elytral intervals in the latter. A very few specimens of *A. jacobinus* from Baja California Norte have less markedly elevated alternate elytral intervals and have shorter dorsal erect vestiture than throughout the rest of the species range and are thus difficult to separate from *A. angularis*. Although these character states are such that they still allow for recognition of these individuals as *A. jacobinus*, they can also be more easily recognized by the robust and less markedly divergent tarsal claws. (See also "Problems in recognition" section for *A. porosus*).

Description.— *Specimens examined.* 218 males, 246 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 11. *Size.* Length, male, 5.7–10.6 mm; female, 6.9–12.2 mm. Width, male, 2.6–5.2 mm; female, 3.0–5.6 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with moderately dense, small to moderately large, deep punctures. Frons and area immediately above eyes with sparse short erect hair-like scales. Area immediately behind posterior margin of eye with large, shallow to deep, irregularly impressed punctures. Area above eyes markedly elevated above rest of frons

(eyes appearing distinctly browed in anterior view). Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.66-0.91 times length in male; 0.62–0.92 in female) (Fig. 85). Median carina slightly to well-developed, low and rounded but distinct, to high and sharp (Fig. 85). Dorsal and lateral punctation small, moderately deep, sparse to moderately dense. Dorsally, excluding epistoma, with dense short, suberect hair-like scales, and dense elongate-narrow to broad appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 85a). Epistoma with apical margin rounded at middle (Fig. 85b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of labial palpus (as in Figs. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins subparallel from base to almost apical one-quarter, then divergent to apical one-quarter (giving a distinctly laterally tuberculate appearance); markedly constricted at acute angle anterior to apical one-quarter, then straight or slightly convergent to apex; widest at tubercles to subequal in width at base and apical one-quarter (Figs. 72–74). Dorsal and lateral punctation moderately large to large, deep, sparse to moderately dense, in some specimens areas between punctures irregularly elevated thus apparently sculptured; punctures sparser and smaller on flanks. Scales white, elongate-narrow to broad, appressed, sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in some specimens); dense laterally in pair of posterolaterally directed arcuate stripes; scales sparser at lateral margins and ventrally on flanks, to uniformly dense laterally, at lateral margins and on flanks, individual large punctures not obscured. Median carina lacking. Dorsally covered throughout with moderately dense, fine, short, erect hair-like scales. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 85a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with moderately to well-developed rounded swelling anterior to each prosternal impression (Fig. 85a). *Elytra.* Moderately robust in general form (width at midlength 0.57-0.76 times length in males; 0.59-0.75 in females) (Figs. 72–74). In dorsal view with lateral margins slightly arcuate throughout length or with margins slightly convergent to subparallel from apical one-third to humerus; humerus rounded to obtuse, not distinct to distinct (Figs. 72–74). Sutural interval and intervals 3, 5, 7, and 9 with moderately dense, short, erect hair-like scales; sparser on other intervals. Dorsally with sutural interval and intervals 3, 5, 7, and 9 slightly to moderately swollen and convex (more so basally in some specimens). Scales elongate-narrow, various in density and size. Pattern extremely various; many specimens with two variously sized posteromedially directed glabrous or nearly so areas, one at basal one-third from intervals 4 to 6, other at apical one-third from intervals 2 to 7, and with various number of scattered small glabrous (or nearly so) patches (Fig. 72); other specimens with glabrous areas of various extent on interval 2 at basal one-quarter and from midlength to apical one-quarter, interval 4 at basal one-third, interval 6 at basal one-quarter and apical one-quarter, and interval 8 at midlength; scales confined to median portion of intervals, striae and immediately adjacent portion of intervals lacking scales (Fig. 73). *Wings.* Absent (95.5%, N=443) or present, long (greater than elytra in length [4.5%, N=21]). Branches of 2A not complete, not joined at base. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes small. Tarsal claws widely divergent, basal internal flange absent (Fig. 66). Ventral tarsal pilose vestiture of foretarsus of male absent from article 1, present as minute apical tufts of article 2, as small apical pads of article 3; of foretarsus of female, mesotarsus of male and female, and metatarsus of female, lacking from articles 1 and 2, present as minute to small pads at apex of article 3; of metatarsus of male lacking from articles 1 and 2, lacking from to present as minute pads at apex of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with moderately dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with moderately dense, individually distinct circular glabrous patches, each with large puncture and single long erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with small dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (nine examined). Abdominal sternum VIII with lateral arms narrow, slightly outwardly arcuate in basal one-half, then parallel to near apex, markedly inwardly arcuate immediately before apex (Fig. 93a). Gonocoxite II with stylus very small, anteapical in position by more or less one-half length of stylus (Fig. 93b). Male (10 examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections (as in Fig. 101e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel-sided throughout length. Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 100a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites lightly sclerotized, each lacking median projection (Fig. 100d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 100a).

Geographic variation.— Geographic variation is extensive in a number of characters in members of this species. As a result there has been a lot of confusion regarding the specific limits of the previously recognized species (the names of which are here placed in synonymy) and identity of various specimens. Specimens I examined bear label notes either indicating a questionable identification or indicating that the specimen represents a probable new species. One manuscript name is also represented on these labels.

Both macropterous and apterous individuals are known. Macropterous individuals have only slightly elevat d and convex alternate elytral intervals and have more or less parallel-sided elytra withdistinct humeri. Apterous individuals on the other hand have alternate elytral intervals that are more markedly elevated and convex, and have elytra with the lateral margins more arcuate with indistinct humeri. There appears to be no geographic component to this variation because macropterous individuals, although few in number, are found throughout most of the species range, with the notable exception of Colorado. This has no doubt contributed to confusion, but the main cause of the confusion is due to the patterns of geographic variation in other structural features. Specimens from eastern and central Colorado, western Oklahoma, and western Texas (called hereafter the "eastern morph" and including typical *Cleonus angularis* LeConte), are different from those to the west in California, Nevada, Utah, and northern Arizona (called hereafter the "western morph" and including typical *Dinocleus denticollis* Casey and *Dinocleus porcatus* Casey).

Eastern morphs (Fig. 73) differ from western morphs (Fig. 72) in states of the following characters: shorter and more robust rostrum; rostral carina higher and sharper; eyes slightly less prominent and convex in dorsal view; pronotal punctures denser, larger, deeper and more irregularly impressed; slightly more markedly elevated alternate elytral intervals; generally a more globose and robust elytral form; elytra with glabrous patches primarily transversely oriented (Fig. 72) not longitudinally oriented (Fig. 73). Specimens from southern Arizona and southern New Mexico however, are not reliably assignable to either form. They are intermediate in many structural features which characterize the eastern and western morphs and it is in this area that apparent intergradation takes place. Elytral scale patterns are not clearly of one or the other form (Fig. 74); rostra are variable in form, and carinae both in form and in degree of elevation; pronotal punctation is variable in depth, density and regularity of impression; and elytral characters (other than scale pattern) are also variable. Based upon this intergradation, I conclude that the eastern and western morphs and the individuals from southern New Mexico and southern Arizona are all conspecific.

It appears that members of certain species of *Apleurus* (and also *Cleonidius*) are largely restricted to sandy habitats such as dune fields, sand hills, dry washes, stream beds, and riparian habitats. These are either localized and discontinuous dune fields, or although widespread, washes and riparian communities restricted in their degree of continuity. Dispersal possibilities are therefore, I believe, markedly influenced by the continuity of drainage patterns or other suitable habitats, and also as is true for all insects, by the presence or absence of wings. Population distinctiveness and apparent lack of intergradation in the north in Colorado and adjacent Utah and northern Arizona, is perhaps due to a combination of a higher continental divide in this area with a more marked discontinuity between eastern and western drainage patterns, consequently more localized and disjunct habitats, and general overall low number of macropterous individuals including presence of only apterous individuals in Colorado. These features may all combine to reduce the probability of dispersal between eastern and western drainages resulting in local selection for differences between the two morphs. On the other hand, this is not so in southern Arizona and New Mexico where the continental divide is much lower, drainage patterns are not as markedly discontinuous and localized and where macropterous individuals although still few in number, are present in both drainages. Dispersal and interbreeding of individuals is therefore possible in this area with the result that there is no local selection for differences between the two drainages.

This pattern is similar to that found in *C. canescens* which also differs between Colorado and adjacent Utah in the north but not so in the south in New Mexico and Arizona, and all individuals of which are brachypterous and incapable of flight. Species which are found in these same areas but which are macropterous do not show distinctive populations on the eastern and western sides of the continental divide.

Geographic distribution.— This species is widespread in the southwestern United States of America from Colorado, western Oklahoma and western Texas, west to Nevada in the north, extreme southern coastal California and Baja California Norte, Mexico in the south (Fig. 211).

Natural history.— This species is associated with grassland, desert-grassland transitional habitats, Pacific semi-desert, and Great Basin, desert. Specimens have been collected in sand dune habitats in California, Arizona, Utah, and New Mexico, and otherwise in dry washes and streambeds throughout the species range. Adults have been collected largely on Compositae as follows: *Chaenactis stevioides* Hook. and Arn., *Chrysothamnus nauseosus* (Pall.) Britton, *C. viscidiflorus* (Hook.) Nutt. var. *pumilis, Gutierrezia lucida* Greene, *G. microcephala* (DC.) Gray, *Aplopappus arcadenius* (Greene) Blake, *A. linearifolius* DC (all Compositae); *Atriplex lentiformis* (Torr.) Wats. (Chenopodiaceae). Adults have also been collected from roots of *Aplopappus tenuisectus* (Greene) Blake and *Psilostrope cooperi* (Gray) Greene (Compositae). It is likely that many shrubby Compositae, especially those on which adults are commonly found, act as hosts for this species. Adults have been collected throughout the year at elevations of from 15–2876 m (N=63) (Fig. 232).

Adults have been collected in the stomach contents of the roadrunner, *Geococcyx californicus* (Aves) at Carlsbad, New Mexico.

Chorological relationships.— This species is sympatric throughout nearly its entire range with *A. albovestitus*; throughout Arizona, New Mexico, and western Texas with *A. lutulentus*; and throughout southeastern Arizona with *A. saginatus*. It is at most narrowly sympatric with its close relatives *A. jacobinus* in southeastern California, and *A. porosus* in Baja California Norte, México.

Phylogenetic relationships.— *Apleurus angularis* is the sister-species of *A. jacobinus* (Fig. 235). Presence of the apotypic state of tarsal claws each lacking a basal internal flange in some *A. porosus* and in *A. angularis* is a result of either hybridization or of homoplasy, more likely the former.

Apleurus (Apleurus) jacobinus (Casey), new combination
(Figs. 67, 71, 86, 94, 101, 208)

Centrocleonus pilosus LeConte 1876a:145 [not Chevrolat 1873:42]. NEW SYNONYMY Holotype (examined), male, labelled "Calif.", "type/ 5240", "*Centrocleonus/ pilosus* Lec." (MCZC). Type locality, California. Henshaw 1881–1882 (check.). Henshaw 1885 (check.).

Dinocleus jacobinus Casey 1891:179. Lectotype (here designated), female, one of eight syntypes, labelled "Cal.", "Casey/ bequest/ 1925", "TYPE USNM/ 37268", "*D./ jacobinus/* Cas." and with my designation label "*Dinocleus/ jacobinus/* Casey LECTOTYPE/ desig. Anderson" (USNM). Type locality, San Diego, California. Fall 1901 (check.). Fall 1913. Leng 1920 (catal.).

Dinocleus pilosus; Casey 1891 (key, redesc.). Fall 1901 (check.). Fall 1913. Leng 1920 (catal.). Essig 1958 (biol., misident. of *Apleurus albovestitus*).

Cleonus (Dinocleus) capillosus Csiki 1934:66. NEW SYNONYMY New name for *Centrocleonus pilosus* LeConte. Blackwelder 1939 (check.).

Cleonus (Dinocleus) jacobinus; Csiki 1934 (catal.).

Cleonus (Dinocleus) pilosus; Csiki 1934 (catal., as jr. homonym).

Cleonis capillosus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis jacobinus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis pilosus; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Notes about synonymy.— Based upon examination of very few specimens, Casey (1891) distinguished *Dinocleus jacobinus* Casey from *Dinocleus pilosus* (LeConte) on the basis of the smaller size, coarser darker and sparser elytral erect vestiture, more parallel-sided elytra with exposed humeri, and less markedly elevated alternate elytral intervals of the former. Having now examined large numbers of individuals I find that unequivocal assignment to either of the forms is not possible because of variation in all but one of the above characters, and conclude that the two forms are conspecific. I can see no differences in degree of coarseness or color of the erect elytral vestiture as noted by Casey (1891).

Problems in recognition.— Many specimens of *A. jacobinus* are confused with individuals of *A. angularis* and *A. porosus*. Characters and their states allowing for the separation of these species from *A. jacobinus* are discussed in the respective "Problems in recognition" sections for those species.

Description.— *Specimens examined.* 123 males, 255 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WElM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 12. *Size.* Length, male, 7.8–11.8 mm; female, 5.8–14.3 mm. Width, male, 3.7–5.5 mm; female, 2.8–6.5 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with sparse to dense, large to very large, deep punctures. Frons and area immediately above eyes with dense very long erect hair-like scales (short or lacking in few specimens). Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes markedly elevated above rest of frons (eyes apparently distinctly browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.67-0.79 times length in male; 0.65-0.80 in female) (Fig. 86). Median carina slightly to well-developed, low to high, rounded, in part obscured in many specimens by large deep punctures (Fig. 86). Dorsal and lateral punctation large to very large, deep, moderately dense to dense. Dorsally, excluding epistoma, with dense very long, erect hair-like scales (short or lacking from few specimens), and dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 86a). Epistoma with apical margin rounded at middle (Fig. 86b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of labial palpus (as in Figs. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins subparallel from base to almost apical one-quarter, then divergent to apical one-quarter (thus distinctly laterally tuberculate in appearance); markedly constricted at acute angle anterior to apical one-quarter, then straight or slightly convergent to apex; widest at tubercles to subequal in width at base and apical one-quarter (Fig. 71). Dorsal and lateral punctation moderately large to large, deep, sparse to moderately dense, in some specimens areas between punctures irregularly elevated thus appearing sculptured; punctures sparser and smaller on flanks. Scales white, elongate-fine to elongate-narrow, appressed, sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in most specimens); dense laterally in pair of posterolaterally directed arcuate stripes; scales sparser at lateral margins and ventrally on flanks, to uniformly dense laterally, at lateral margins and on flanks, not obscuring individual large punctures. Median carina absent to present and distinct in some specimens. Dorsally covered throughout with sparse to moderately dense, fine, very long, erect hair-like scales, each situated in large puncture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 86a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 86a). *Elytra.* Moderately robust in general form (width at midlength 0.65-0.75 times length in males; 0.61–0.76 in females) (Fig. 71). In dorsal view with lateral margins slightly arcuate throughout length; humerus rounded, not distinct (Fig. 71). Sutural interval and intervals 3, 5, 7, and 9 with dense, very long, erect hair-like scales; sparser and slightly shorter on other intervals (short or lacking in some specimens). Dorsally with sutural interval and intervals 3, 5, 7, and 9 moderately to markedly swollen and convex (interval 5 at basal one-third and intervals 7 and 9 near base only slightly swollen in some specimens). Scales elongate-narrow, various in density and size; pattern slightly various, but generally with two variously sized posteromedially directed glabrous or nearly so areas, one at basal one-third from intervals 4 to 6, other at apical one-third from intervals 2 to 7, and with various number of scattered small glabrous or nearly so patches (Fig. 71). *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large to large, metatibial uncus of both sexes small. Tarsal claws slightly divergent, basal internal flange present, slightly to well-developed (Fig. 67). Ventral tarsal pilose vestiture of foretarsus of male absent of article 1, present as minute apical tufts of article 2, as small apical pads to moderately large pads on apical one-third of article 3; of foretarsus of female, lacking from article 1, present as minute to small pads at apex of articles 2 and 3; of mesotarsus and metatarsus of male, lacking from all three articles to as minute apical pads of article 2, and as small apical pads to moderately large pads on apical one-third of article 3; of mesotarsus and metatarsus of female, lacking from articles 1 and 2, present as minute apical tufts of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not at all tumescent (as in Fig. 59). *Abdomen.* Ventral surface with moderately dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV)

with moderately dense, individually distinct circular glabrous patches, each with large puncture and single long erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with small dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (six examined). Abdominal sternum VIII with lateral arms narrow, slightly outwardly arcuate in basal one-half, then parallel to near apex, markedly inwardly arcuate immediately before apex (Fig. 94a). Gonocoxite II with stylus very small, anteapical in position by more or less one-half length of stylus (Fig. 94b). Male (seven examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections (Fig. 101e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel-sided throughout length. Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 101a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites lightly sclerotized, each lacking median projection (Fig. 101d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 101a).

Geographic variation.— Specimens from the southern part of the species range in extreme southern California and Baja California Norte, México have shorter and sparser dorsal erect vestiture than do individuals from the northern inland portions of the range. These same specimens tend to have the elytral intervals less markedly elevated throughout (Baja California Norte) or have only intervals 5 and 7 variously swollen basally (extreme southern California). Tarsal claws of the Baja California Norte individuals, although robust and not widely divergent, each have only a slightly developed basal internal flange. All of these southern individuals possess distinct glabrous patches on the abdominal sterna.

Two specimens from Point Reyes National Seashore and two specimens from Redwoods Regional Park near Oakland lack or else have extremely short dorsal erect vestiture (apparently not due to abrasion), but otherwise are typical *A. jacobinus.*

Geographic distribution.— This species is found in California from the San Francisco Bay area south through coastal and central California to northern coastal Baja California Norte, Mexico (Fig. 208).

Natural history.— This species is associated exclusively with Pacific semi-desert habitat. Adults of have been collected on *Aster* sp., *Hemizonia* sp., *H. pungens* (H. and A.) T. and G. (Compositae); beans (Leguminosae); *Gossypium hirsutum* L. (cotton; Malvaceae); and carrots (Umbelliferae). They have also been found in various shipments of beans and raisins. Definite hosts are not known. Adults have been collected throughout the year at elevations of from 5–424 m (N=15) (Fig. 232).

Chorological relationships.— This species is sympatric throughout its range with western *A. albovestitus*, and is at most narrowly sympatric with southern Californian *A. angularis* and *A. porosus* from southern California or northern Baja California Norte, México.

Phylogenetic relationships.— *Apleurus jacobinus* is the sister-species of *A. angularis* (Fig. 235).

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Apleurus (Apleurus) albovestitus (Casey), new combination
(Figs. 75–79, 88, 95, 103, 209)

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Cleonus molitor LeConte 1858:78 [not Gyllenhal 1834:174]. NEW SYNONYMY Holotype (examined), female, labelled with a gold circle (=California), "*Cleonus/ molitor/* Lec.", "Type/ 5183", "Anobium!/ parasitic!" (MCZC). Type locality, California. Gemminger and von Harold 1871 (catal.).
Centrocleonus molitor; LeConte 1876a (key, diag.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889.
Dinocleus albovestitus Casey 1891:183. Lectotype (here designated), male, one of an undetermined number of syntypes, labelled "Los Angeles/ Co. CAL", "TYPE USNM/ 37273", "CASEY/ bequest/ 1925", "*D./ albovestitus/* Cas." and with my designation label "*Dinocleus albovestitus/* Csy. LECTOTYPE/ desig. Anderson" and genitalia in microvial under labels (USNM). Type locality, Los Angeles, California. Fall 1901 (check.). Casey 1904. Leng 1920 (catal.). Ting 1936 (morphol.). Bruhn 1947 (morphol.). Sanders 1960 (morphol.).

Dinocleus densus Casey 1891:185. NEW SYNONYMY Lectotype (here designated), male, one of four syntypes, labelled "Winslow", "CASEY/ bequest/ 1925", "TYPE USNM/ 37277", "*D./ densus/* Cas." and with my designation label "*Dinocleus/ densus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Winslow, Arizona. Wickham 1896 (check.). Leng 1920 (catal.).

Dinocleus molitor; Casey 1891 (key, redesc.). Fall 1901 (check.). Champion 1902–1906 (syn., distn.). Casey 1904. Leng 1920 (catal.).

Dinocleus wickhami Casey 1891:184. NEW SYNONYMY Holotype (examined), male, labelled "Indio/ California/ Wickham", "CASEY/ bequest/ 1925", "TYPE USNM/ 37276", "*D./ wickhami/* Cas." (USNM). Type locality, Indio, California. Fall 1901 (check.). Leng 1920 (catal.). Tanner 1934 (check.).

Dinocleus interruptus Casey 1904:322 [not Zoubkoff 1829:162]. NEW SYNONYMY Lectotype (here designated), male, one of three syntypes, labelled "Ut", "CASEY/ bequest/ 1925", "TYPE USNM/ 37274", "*interruptus*" and with my designation label "*Dinocleus/ interruptus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Utah. Leng 1920 (catal.).

Dinocleus mexicanus Casey 1904:322. NEW SYNONYMY Lectotype (here designated), male, one of two syntypes, labelled "Guer.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37275", "*mexicanus*" and with my designation label "*Dinocleus/ mexicanus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Guerrero, México. Champion 1902–1906 (distn.).

Cleonus (Dinocleus) albovestitus; Csiki 1934 (catal.).

Cleonus (Dinocleus) densus; Csiki 1934 (catal.).

Cleonus (Dinocleus) interruptus; Csiki 1934 (catal.).

Cleonus (Dinocleus) mexicanus; Csiki 1934 (catal.).

Cleonus (Dinocleus) structor Csiki 1934:67. NEW SYNONYMY New name for *Cleonus molitor* LeConte. Blackwelder 1939 (check.).

Cleonus (Dinocleus) wickhami; Csiki 1934 (catal.).

Cleonus mexicanus; Blackwelder 1947 (check.).

Dinocleus pilosus; Essig 1958 (biol., misident.).

Cleonus albovestitus; Hardy and Andrews 1976 (distn., biol.). Andrews *et al.* 1979 (distn., biol.).

Cleonis albovestitus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis densus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis interruptus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis mexicanus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis molitor; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Cleonis structor; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis wickhami; O'Brien and Wibmer 1982 (catal., distn.).

molitor, incertae sedis; Chevrolat 1873.

Notes about synonymy.— I consider *A. albovestitus* to be composed of a number of largely allopatric morphotypes most of which are distinguished solely on the basis of patterns of surface vestiture (Figs. 75–79), but which exhibit continuous intergradation in zones of parapatry or narrow sympatry (see "Geographic variation" section).

One of these morphotypes is largely black and glabrous, most of the surface vestiture having been abraded (Figs. 78–79). This is *Centrocleonus molitor* LeConte. *Dinocleus mexicanus* Casey is a form of this same morphotype, but in which the scales have not been extensively abraded. *Dinocleus densus* Casey, is a form in which there has been no abrasion of scales. This morphotype is confined to the Colorado and Gila River drainages.

The second morphotype, that with dense elytral and ventral abdominal scales and lacking abdominal glabrous patches but with small elytral glabrous patches, includes *Dinocleus interruptus* Casey, *D. wickhami* Casey, and *D. albovestitus* Casey (Figs. 76–77).

The third morphotype is recognized, among other characters, by the larger and more numerous elytral and abdominal glabrous patches (Fig. 75).

Since I have been unable to find other structural features which correlate with the variation in patterns of surface vestiture to allow for reliable separation of the various morphotypes, I conclude that a single species is present, but with allopatric forms having different locally adaptive patterns of surface vestiture.

Champion (1902–1906) incorrectly stated that *D. mexicanus* Casey is a new name for *Centrocleonus molitor* LeConte.

Problems in recognition.— Individuals of *A. albovestitus* might only be confused with those of *A. saginatus* although key characters should serve to reliably separate all members of the two species. Special note should be made of the marked secondary sexual dimorphism in extent of ventral tarsal vestiture in *A. saginatus* that is not as marked in *A. albovestitus*. This allows for easy recognition of males of *A. saginatus*.

All *A. albovestitus* that possess glabrous ventral abdominal patches are found only in western California; those *A. albovestitus* found sympatrically with *A. saginatus* have extremely dense scales on the abdominal sterna and lack the glabrous patches present in all *A. saginatus*.

Description.— *Specimens examined.* 1251 males, 1470 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 13. *Size.* Length, male, 11.8–16.8 mm; female, 12.8–21.4 mm. Width, male, 5.1–7.2 mm; female, 5.4–8.8 mm. *Head.* Eye slightly prominent and convex in dorsal view. Frons and vertex with sparse to moderately dense, small, shallow punctures. Frons largely lacking suberect or erect vestiture, with at most only sparse, small suberect scales immediately above eyes. Area immediately behind posterior margin of eye with small, shallow to moderately deep, irregularly impressed punctures. Area above eyes continuous with and not elevated above rest of frons (eyes not browed in anterior view). Width of frons greater than to subequal in width to apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.62–0.78 times length in male; 0.63–0.79 in female) (Fig. 88). Median carina lacking. Dorsal and lateral punctation small to moderately large, moderately deep, sparse to moderately dense. Dorsally, excluding epistoma, either lacking suberect or erect vestiture or with at most scattered short suberect scales; and lacking (abraded) or with dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig 88a). Epistoma with apical margin rounded at middle (Fig. 88b). *Mouthparts.* Maxillary palpus with stipes with large seta on outer margin (as in Fig. 64). Labial palpi separated by more or less width of basal article of labial palpus (as in Fig. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins straight and subparallel to slightly convergent from base to almost apical one-quarter, not to slightly expanded laterally at apical one-quarter (thus indistinctly laterally tuberculate in appearance); moderately constricted at obtuse to subacute angle anterior to apical one-quarter, then straight and slightly convergent to apex; widest at base to subequal in width at base and apical one-quarter (Figs. 75–79). Dorsal and lateral punctation small, shallow, sparse to moderately dense; punctures sparser on flanks; outer margins of larger punctures not swollen or glabrous. Scales white, elongate-narrow to broad, appressed, entirely lacking (abraded) to sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in most specimens); very dense laterally and ventrally on flanks onto prosternum; scales sparser at lateral margins. Median carina lacking to present but irregularly developed but with at least a broad low rounded median swelling in most specimens. Dorsally lacking suberect or erect vestiture or with sparse, short, erect hair-like scales, each situated in large puncture. Anterolateral margin with postocular projection slightly to moderately developed (Fig. 88a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 88a). *Elytra.* Moderately robust to moderately elongate-narrow in general form (width at midlength 0.59-0.72 times length in males; 0.56-0.69 in females) (Figs. 75–79). In dorsal view with lateral margins straight, slightly convergent to divergent from apical one-third to humerus; humerus rounded to obtuse, indistinct to distinct, with at most only very few small glabrous shiny tubercles. Dorsal suberect or erect vestiture lacking to sparse, short and fine. Dorsally with all intervals flat. Scales, if present, elongate-narrow to elongate-fine, white to golden. Scale pattern extremely various; with scales entirely or largely lacking (abraded) except near apex on declivity (Figs. 78–79), to present to various extent (not abraded), uniformly dense and large on sutural interval and intervals 3, 5, 7, and 9, uniformly sparse and small on intervals 2, 4, 6, and 8, distinct glabrous patches absent (Fig. 77); or, to scales not abraded, uniformly dense and large on sutural interval and intervals 3, 5, 7, and 9, and sparse and small to various degree on intervals 2, 4, 6, and 8, with at most scattered but few glabrous patches present (Fig. 76); or, to sutural interval with scales sparse and small or large and dense, otherwise with scales of elytral intervals extremely various in size and density, with numerous irregularly distributed small and moderately large glabrous or nearly so patches present (Fig. 75). *Wings.* Short (slightly shorter than elytra in length [0.2%, N=4]), to long (slightly greater than elytra in length [99.8%, N=1717]). Branches of 2A complete and joined at base. *Legs.* Foretibia of female with inner margin with small to minute denticles in apical one-third; subapical tooth minute, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large to large, metatibial uncus of both sexes small. Tarsal claws slightly divergent, basal internal flange present, well-developed (as in Fig. 67). Ventral tarsal pilose vestiture of foretarsus of male absent to present as minute apical tufts on articles 1 to 3; of mesotarsus of male, lacking from articles 1 and 2, present as minute apical tufts of article 3; lacking from articles 1 to 3 of all tarsi of female and from articles 1 to 3 of metatarsus of male. *Mesosternum.* Mesosternal process flat to very slightly convex but not at all tumescent (as in Fig. 59). *Abdomen.* Ventral surface either with scales present, white, appressed, along posterior margins of abdominal sterna, also with scattered, suberect short hair-like scales, each situated in large puncture; or, with white appressed scales uniformly very dense, abdominal sterna III to VI without glabrous patches to with scales moderately dense, individually distinct circular glabrous patches present (especially on abdominal sterna III and IV), each with large puncture and single short suberect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with large dorsally directed median truncate tooth. Abdominal

tergum VII of female slightly medially longitudinally carinate, apical margin moderately elevated and reflexed; abdominal tergum VIII of female markedly medially longitudinally carinate, apical margin moderately elevated and reflexed. *Genitalia*. Female (12 examined). Abdominal sternum VIII with lateral arms broad, straight and slightly divergent from base to apical one-third, slightly inwardly arcuate from apical one-third to apex (Fig. 95a). Gonocoxite II with stylus absent, with darkly sclerotized slightly elevated dorsal subapical ridge (Fig. 95b). Male (eight examined). Abdominal sternum VIII with paired sclerite with inner apices with well-developed ventral projections (Fig. 103e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel-sided throughout length. Internal sac short and high, slightly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe near dorsal margin at midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 103a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites darkly sclerotized, each with long dorsoapically directed median projection (Fig. 103d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 103a).

Geographic variation.— Variation in the pattern of surface vestiture in members of this species is very extensive (Figs. 75–79). There is also slight variation in other structural features but these could not be reliably correlated with the variation in vestiture to allow recognition of more than one species (see also "Notes about synonymy" section). However, I recognize three largely allopatric or parapatric morphotypes. In the first of these, vestiture is abraded or at least subject to abrasion. Such specimens are primarily black and glabrous (except for the tibiae and tarsi) and possess moderately dense to dense scales only along the lateral margins of the elytra and the posterior margins of the abdominal sterna (especially V and VI), and to a various extent in some specimens, also in the apical one-third of the elytra, onto the elytral declivity (Figs. 78–79). Scattered single scales are also found variably on the thoracic and abdominal sterna, elytra and femora. In individuals in which scales are variably present on the elytra, the scales are uniformly dense and large on all intervals to slightly less dense and smaller on intervals 2, 4, and 6. Scales are very easily abraded on these specimens. Individuals of this morphotype have been collected at elevations of from -67–870 m (N=23).

This form is found throughout the southern portion of the Colorado River drainage, the western portion of the Gila River drainage, and throughout Imperial County, California. Individuals from the latter area tend to have the elytral scales denser and not abraded and although lacking distinct glabrous elytral patches, the general scale pattern clearly grades into that pattern to be discussed next in which small elytral glabrous patches are present (Fig. 76). Individuals of this morphotype seem restricted to *Pluchea sericea* (Nutt.) Coville (Compositae) in sand dune habitats along the margins of waterways in these areas.

A second form of *A. albovestitus* is also found in these and other areas, and although the ranges of the two morphotypes narrowly overlap, they have not been collected together at the same time and place. Individuals of this form possess large and dense elytral surface vestiture that is not prone to abrasion. All abdominal sterna have uniformly very dense scales; no glabrous patches are present. Elytral scales are uniformly large and dense to very dense, but are lacking or very sparse in scattered small to moderately large patches on elytral intervals 2 to 8 (Fig. 76). Scales of the sutural interval of many of these specimens are uniformly small and sparse. Punctures of elytral striae are small and indistinct. This form is widespread from Nevada and Utah south to extreme western Texas, New Mexico, Arizona and southeastern California, south into Baja California Sur, Mexico. Individuals of this form in Utah and northern Arizona, along the northern Colorado and Virgin River drainages, differ from those elsewhere by largely lacking glabrous or nearly so patches on the elytra (Fig. 77). Scales of some individuals in these areas are less dense and smaller on intervals 2, 4, and 6, much the same pattern as in specimens of the largely glabrous morphotype in which elytral scales have not been extensively abraded. This similarity in scale pattern suggests the notion that the largely glabrous individuals of morphotype 1 in the southern portion of the Colorado River

drainage may have reached this area as a result of downriver dispersal from parent populations along the Virgin and northern Colorado Rivers. Individuals of this morphotype have been collected at elevations of from 2–1446 m (N=49).

A third pattern of vesture is found in individuals from southern coastal to northern coastal and central California. In this form, scales of the elytra are less dense and smaller than in the previous forms, and the elytral glabrous or nearly so patches are generally larger and more numerous (Fig. 75). Punctures of the elytral striae are generally slightly larger and more distinct than in the other morphotypes. Abdominal sterna (especially III and IV) of many individuals with this elytral scale pattern possess small to moderately large indistinct to distinct glabrous areas, each with a single short suberect hair-like scale situated in the center. Suberect vesture, lacking from the elytra on the other morphotypes, is short, sparse and fine on the elytra of many of these specimens. Elytral scale patterns of this and of the second morphotype completely intergrade in southern California. Individuals of this third morphotype have been collected at elevations of from -41–3185 m (N=61).

The potential adaptive significance of variation in surface vesture is not known but is suspected to be influenced by thermoregulatory effects, or, more likely, by cryptic effects resulting from similarity in color and pattern to the ground substrate (see "Evolutionary Trends" section).

Brachypterous specimens of *A. albovestitus* are only known from two localities in Baja California Norte, México.

Geographic distribution.— This species is distributed from New Mexico and western Texas west through Utah and Nevada to northern California in the north, through Arizona and extreme northwestern México to southern California and Baja California Sur, México in the south (Fig. 209).

Natural history.— This species is associated with a variety of habitats as follows; desert-grassland transitional, Pacific semi-desert, and Great Basin, Chihuahuan, Mojave, and Sonoran deserts. Adults of this species have been collected in sand dune habitats in California, Arizona, Utah, Nevada (label data; Andrews *et al.* 1979; Hardy and Andrews 1976) and otherwise primarily in dry washes and stream beds throughout the species range. Andrews *et al.* 1979 tentatively suggest that the species is an obligate sand associate.

Adults have been collected on a wide variety of plants as follows: *Ephedra* sp., *E. californica* Wats. (Ephedraceae); *Ambrosia* sp., *A. psilostachya* DC., *Artemesia tridentata* Nutt., *Baileya multiradiata* Harv. and Gray, *B. pleniradiata* Harv. and Gray, *Baccharis glutinosa* Pers., *Chrysothamnus nauseosus* (Pall.) Britton, *Dicoria* sp., *Franseria* sp., *F. confertiflora* (DC.) Rydb., *F. dumosa* Gray, *Flourensia cernua* DC., *Gutierrezia microcephala* (DC.) Gray, *Aplopappus acradenius* (Greene) Blake, *Hymenoclea* sp., *H. salsola* T. and G., *Hymenothrix wislizeni* Gray, "*Palafoxia arida*", *P. linearis* (Cav.) Lag., *Pluchea sericea* (Nutt.) Coville, *Verbesina enceloides* (Cav.) Benth. and Hook., *Xanthium* sp., (all Compositae); *Larrea tridentata* (DC.) Coville (Zygophyllaceae); *Hordeum* sp., *Sitanion* sp., (Graminae); *Datura* sp., (Solanaceae); *Gossypium* sp., (Malvaceae); *Eriogonum fasciculatum* Benth. var. *polifolium* (Polygonaceae); *Astragalus* sp., *Cercidium floridum* Benth., *Medicago sativa* L., *Olneya tesota* Gray, *Prosopis juliflora* (Swartz) DC. (all Leguminosae); *Atriplex* sp., *A. lentiformis* (Torr.) Wats., *Salsola kali* L., *Sarcobatus vermiculatus* (Hook.) Torr. (all Chenopodiaceae); *Vitus* sp. (Vitaceae); *Prunus persica* Batsch. (peach; Rosaceae); *Raphanus sativus* L. (radish; Cruciferae). No definite hosts are known, but the vast majority of plant association are with Compositae; records of occurrence on members of other families are

generally single instances of but one or two individuals and very likely represent chance occurrences. I suspect that a wide variety of Compositae serve as host plants for this species.

Adults have been collected throughout the year at elevations from -67–3185 m (N = 133) (Fig. 232).

As noted in the "Geographic variation" section, individuals of each of the three morphotypes occur over slightly different elevational ranges.

Chorological relationships.— This species is sympatric with *A. lutulentus* in Arizona, New Mexico and western Texas; with *A. angularis* throughout most of its range, with the exception of northern California; with *A. jacobinus* throughout entire range of that species in California; narrowly sympatric with *A. porosus* in Baja California Norte, México and southern California; and sympatric with its sister-species *A. saginatus* throughout Arizona, southern New Mexico, and extreme nothwestern México.

I have caught large numbers of specimens of *A. albovestitus* together with *A. lutulentus* on *Chrysothamnus nauseosus* (Compositae) in the vicinity of Portal, Arizona and Animas, New Mexico.

Phylogenetic relationships.— *Apleurus albovestitus* and *A. saginatus* are sister-species (Fig. 235).

Apleurus (Apleurus) saginatus (Casey), new combination
(Figs. 63–64, 80, 87, 96, 104, 206)

Dinocleus saginatus Casey 1891:182. Holotype (examined), male, labelled "Ariz.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37272", "*D./ saginatus*/ Cas." (USNM). Type locality, Arizona. Leng 1920 (catal.).
Dinocleus dentatus Champion 1902–1906:100. NEW SYNONYMY Holotype (examined), female, labelled "Type", inverted "Sp. figured", "Pinos Altos/ Chihuahua,/ Mexico/ Buchan-Hepburn", "B.C.A. Col. IV.4./ *Dinocleus/ dentatus,*/ Champ.", inverted "*dentatus*, Ch." (BMNH).Type locality, Pinos Altos, Chihuahua, Mexico.
Cleonus (Dinocleus) dentatus; Csiki 1934 (catal.).
Cleonus dentatus; Blackwelder 1947 (check.).
Cleonus (Dinocleus) saginatus; Csiki 1934 (catal.).
Cleonis dentatus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis saginatus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Following examination of types and numerous specimens I regard *Dinocleus saginatus* Casey and *D. dentatus* Casey as conspecific.

Problems in recognition.— Individuals of this species might only be confused with those of *A. albovestitus* (see "Problems in recognition" section for *A. albovestitus*).

Description.— *Specimens examined.* 597 males, 657 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 14. *Size.* Length, male, 14.9–19.5 mm; female, 15.9–21.8 mm. Width, male, 5.8–8.0 mm; female, 6.2–9.0 mm. *Head.* Eye slightly prominent and convex in dorsal view. Frons and vertex with sparse, small, shallow punctures. Frons largely lacking suberect or erect vestiture, with at most only sparse, small suberect scales immediately above eyes; white elongate-narrow appressed scales dense above eyes, sparser medially. Area immediately behind posterior margin of eye with small, shallow to moderately deep, irregularly impressed punctures. Area above eyes continuous with and not elevated above rest of frons (eyes not browed in anterior view). Width of frons greater than to subequal in width to apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.63–0.73 times length in male; 0.63–0.74 in female) (Fig. 87). Median carina lacking to variously developed as low rounded to sharp fine glabrous line. Dorsal and lateral punctation small, shallow, sparse. Dorsally, excluding epistoma, with short scattered suberect scales; and with dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 87a). Epistoma with apical margin rounded at middle (Fig. 87b). *Mouthparts.* Maxillary palpus with stipes with large seta on outer margin (Fig. 64). Labial palpi separated by more or less width of basal article of labial palpus (Fig. 63). Prementum with two or three pairs of large setae (Fig. 63). *Pronotum.* In dorsal view with lateral margins slightly arcuate to straight and subparallel to slightly convergent from base to almost apical one-quarter, not to slightly expanded laterally at apical one-quarter (thus indistinctly laterally tuberculate in appearance); moderately constricted at obtuse to subacute angle anterior to apical one-quarter, then straight and slightly convergent to apex; widest at base to subequal in width at base

and apical one-quarter (Fig. 80). Dorsal and lateral punctation small, shallow, sparse to moderately dense; punctures sparser and shallower on flanks; outer margins of larger punctures swollen, glabrous and shiny (appearing as small tubercles). Scales white, elongate-narrow to broad, appressed sparse and small or lacking medially on disk in broad, apically narrowed patch (except for midline in most specimens); very dense laterally and ventrally on flanks onto prosternum; scales sparser at lateral margins. Median carina lacking to present and irregularly developed in basal one-half as low, broad glabrous line. Dorsally with sparse, short, erect hair-like scales, each situated in large puncture. Anterolateral margin with postocular projection slightly developed (Fig. 87a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 87a). *Elytra.* Moderately robust to moderately elongate-narrow in general form (width at midlength 0.59-0.62 times length in males; 0.56-0.64 in females) (Fig. 80). In dorsal view with lateral margins straight or nearly so, slightly convergent from apical one-third to humerus; humerus obtuse, distinct, with numerous distinct small shiny tubercles (also present at bases of adjacent elytral intervals) (Fig. 80). Dorsal suberect or erect vestiture lacking. Dorsally with all intervals flat. Scales appressed, white to golden in color, various in size and density. Scale pattern various, with numerous small irregularly distributed glabrous or nearly so patches (Fig. 80). *Wings.* Long (slightly greater than elytra in length). Branches of 2A complete and joined at base. *Legs.* Foretibia of female with inner margin with small to minute denticles in apical one-third; subapical tooth minute to small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large to large, metatibial uncus of both sexes small. Tarsal claws slightly divergent, basal internal flange present, well-developed (as in Fig. 67). Ventral tarsal pilose vestiture of foretarsus of male present as small rounded apical pads of article 1, as moderately large rounded pads on apical one-half of article 2, and as large rounded pads on apical one-half of article 3; of foretarsus of female, lacking from articles 1 and 2, present as minute apical tufts of article 3; of mesotarsus of male, absent to present as minute apical tufts of article 1, present as small apical pads of article 2, and present as moderately large round pads on apical one-third of article 3; of metatarsus of male, absent from article 1, present as minute apical tufts of article 2, and present as small apical pads of article 3; lacking from articles 1 to 3 of mesotarsus and metatarsus of female. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with very dense elongate-narrow to broad, white, appressed scales; abdominal sterna III to VI (especially III and IV) with moderately dense individually distinct large circular glabrous shiny patches, each with large puncture and single short suberect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with large dorsally directed median truncate tooth. Abdominal tergum VII of female slightly medially longitudinally carinate, apical margin moderately elevated and reflexed; abdominal tergum VIII of female markedly medially longitudinally carinate, apical margin moderately elevated and reflexed. *Genitalia.* Female (six examined). Abdominal sternum VIII with lateral arms broad, straight and slightly divergent from base to near apex, slightly inwardly arcuate near apex (Fig. 96a). Gonocoxite II with stylus absent, with darkly sclerotized slightly elevated dorsal subapical ridge (Fig. 96b). Male (six examined). Abdominal sternum VIII with paired sclerite with inner apices with well-developed ventral projections (as in Fig. 103e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel sided throughout length. Internal sac short and high, slightly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe near dorsal margin at midlength (Figs. 104a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites darkly sclerotized, each with long dorsoapically directed median projection (Fig. 104d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 104a).

Geographic distribution.— This species is found in southeastern Arizona and extreme southwestern New Mexico, south into northwestern Mexico (Fig. 206).

Natural history.— This species appears restricted to dry washes and riparian habitats in the desert-grassland transitional habitat bordering the eastern Sonoran desert region. Adults have been collected on *Baccharis glutinosa* Pers., *Chrysothamnus nauseosus* (Pall.) Britton, *Hymenoclea monogyra* Torr. and Gray (all Compositae). Definite hosts are not known. Adults have been collected throughout the year at elevations of from 283–1820 m (N = 36) (Fig. 232).

Chorological relationships.— This species is sympatric throughout its range with *A. angularis*, *A. lutulentus*, and its sister-species *A. albovestitus*. I know of no records of *A. saginatus* being caught with any of these three species.

Phylogenetic relationships.— *Apleurus saginatus* and *A. albovestitus* are sister-species (Fig. 235).

Genus *Cleonidius* Casey

Curculio; Pallas 1781 (sp. desc.). Herbst 1795.
Cleonus; Say 1831 (sp. desc.). Melsheimer 1853 (in part; check.). Gemminger and von Harold 1871 (in part; catal.).
    LeConte 1876a (key, sp. descs.). Henshaw 1881–1882 (check.). LeConte and Horn 1883 (key). Henshaw 1885

(check.). Wickham 1899. Wickham 1896 (check.). Fall 1897 (sp. desc.). Fall 1901 (check.). Wickham 1902 (check.). Fletcher 1906. Fall and Cockerell 1907 (in part; check.). Pierce 1907 (biol.). Chittenden 1911 (biol.). Ely 1913 (biol.). Gibson 1914. Anderson 1914. Blatchley and Leng 1916 (key, sp. redescs.). Yothers 1916. Leng 1920 (in part; catal.). Leonard 1926 (in part; check.). Böving 1927 (in part; larval key). Bradley 1930 (in part; key). Wilcox *et al.* 1934. Brimley 1938 (check.). Blackwelder 1947 (in part; check.). Bruhn 1947 (morphol.). Essig 1958 (biol.). Sanders 1960 (morphol.). Tanner 1966 (in part; sp. redesc., biol.). Kingsolver 1972. Kumar *et al.* 1976 (biol.). Arnett *et al.* 1980 (key, biol.).

Rhynchophorus; Say 1831 (in part; sp. desc.).

Cleonis; Kirby 1837 (sp. desc.). O'Brien and Wibmer 1982 (catal., distn.). O'Brien and Wibmer 1984 (in part).

Lixus; Zoubkoff 1833 (sp. desc.). Boheman 1836 (sp. desc.). Randall 1838 (in part; sp. desc.). Mannerheim 1843 (sp. desc.). Motschulsky 1845 (sp. desc.). Gemminger and von Harold 1871 (in part; catal.). Capiomont and Leprieur 1874 (sp. redesc.). Sprague and Austin 1875. LeConte 1876a (in part; key, sp. descs.). Henshaw 1881–1882 (in part; check.). LeConte and Horn 1883 (in part; key). Henshaw 1885 (in part; check.). Wickham 1889. Faust 1890. Casey 1891 (in part; key). Horn 1894 (in part; check.). Petri 1905 (key). Petri 1912. Blatchley 1914 (sp. desc.). Blatchley and Leng 1916 (in part; key, sp. redesc.). Leng 1920 (in part; catal.). Lukjanovitsh 1926. Blatchley 1930. Bradley 1930 (in part; key). Arnett 1960–1962 (in part; key). Kissinger 1964 (in part; key).

Apleurus; Chevrolat 1873 (in part, espèces lyxiformes; check., key, sp. descs.).

Cleonidius Casey 1891:186. As subgenus of *Cleonus*. Gender, masculine. Type species *Cleonis vittatus* Kirby (= *Lixus poricollis* Mannerheim) by subsequent designation (Faust 1904:190). Champion 1902–1906 (sp. redesc.). Csiki 1934 (catal.). Blackwelder 1939 (check.). Arnett 1960–1962 (key, catal.). Kissinger 1964 (key). Hatch 1971 (key, sp. redescs.)

Cleonidius; Faust 1904 (key, check., type species desig.).

Lixestus Reitter 1916:89. As subgenus of *Lixus*. NEW SYNONYMY. Gender, masculine. Type species *Curculio vibex* Pallas by monotypy. Csiki 1934 (catal.).

Lixus (Lixesthus); Ter-Minasyan 1978 (error, misspelling).

Notes about synonymy.— The subgenus *Cleonidius* was first proposed by Casey (1891) to accomodate those *Cleonus* with a cylindrical rostrum, more or less vittate elytral scale pattern, and an elongate-narrow body form approaching that of *Lixus*. Indeed species of *Cleonidius* very closely resemble *Lixus* and species of the two genera are often difficult to separate. This is evidenced by the placement of some species, now regarded as *Cleonidius*, originally in *Lixus*, and by the herein proposed new synonymy of *Lixestus* Reitter, a subgenus of *Lixus*, with *Cleonidius*.

Among *Lixus* species examined, only *Lixus (Lixestus) vibex* Pallas (type species of *Lixestus*), was found to possess a small dorsal median tubercle at the basal margin of variously abdominal sterna V to VII, that is characteristic of *Cleonidius*. However, other *Lixus* species, as yet not examined for this character, may also prove to require inclusion in *Cleonidius* should they possess the apotypic state as noted above. This is not surprising given the similarity of the two genera, their apparent close phylogenetic relationship, and previous lack of consideration of *Cleonidius* species in past studies and resulting classifications of Palearctic *Lixus* species. Thus there is the need for a reevaluation of the validity of at least the subgeneric groupings of *Lixus* in this light. Whether *Cleonidius* will remain as a valid genus when this is done remains to be seen; undoubtedly *Lixus* species will require reclassification.

Prior to the present study, *Cleonidius* had been given generic status by Faust (1904), only.

Diagnosis.— Adult Cleoninae with elongate-narrow to moderately robust body form (Figs. 118–136). Eye more or less oval to elongate-oval, flat (Figs. 137–156). Rostrum elongate-narrow to moderately robust, with at most only low median carina (indicated in the majority of species by low glabrous shiny line) (Figs. 137–156). Antennal funiculus with article 1 longer than article 2; article 2 more or less as wide as long (Figs. 137–156). Pronotal postocular lobes lacking to present and well-developed; postocular vibrissae uniformly short to long but of unequal length, longest immediately behind base of eye (Figs. 137–156). Pronotal disk slightly to distinctly vittate, with white scales largest and/or densest immediately laterad of midline, smaller and/or sparser laterally; largely whitish in color, underlying dark cuticle largely obscured by white scales (Figs. 118–136). Prosternal swellings absent or present, if

present, situated immediately anterior to each procoxal cavity (Fig. 8). Ventral tarsal pilosity extensive (covering greater part of ventral surface of each tarsal article) to reduced in extent or lacking from at least the basal tarsal articles of some species. Tibia with corbel ridge rounded (Fig. 5). Abdominal sternum VII (at least) of females dorsally (internally) with variously developed basal median glabrous shiny tubercle, evident externally as shallow impression. Abdominal sternum VIII of female with basal arm short to long (Figs. 157–176).

Description.— *Size.* Small to moderately large; elongate-narrow to moderately robust in general body form (Figs. 118–136). *Mouthparts.* Prementum flat to slightly swollen ventrally; with as many as three large setae on each side. Maxillary palpus with palpifer and stipes each with at least one large seta. Labial palpi separated by distance subequal to width of basal article of labial palpus. *Rostrum.* Elongate-narrow to robust, not to markedly medially tumescent, with at most only low median carina indicated in majority of species by fine glabrous shiny line (Figs. 137–156). Epistoma not to moderately swollen, with apical margin emarginate medially (Figs. 137b-156b). Antenna with funiculus with article 1 longer than article 2; article 2 more or less as long as wide; apical three articles of club lacking placoidal sensillae. *Head.* Eye oval to elongate-oval; flat (Figs. 137–156). Upper margin of eye rounded, frons flat to variously convex. *Vestiture.* Dorsum with suberect to erect vestiture absent to present and dense, short to very long in length; with simple appressed white scales of various size and density. *Pronotum.* Dorsal surface punctate, median basal area shallowly to deeply impressed; disk with or without various other impressions. Pronotal disk slightly to distinctly vittate, with white scales largest and/or densest immediately laterad of midline, smaller and/or sparser laterally; largely whitish in color, underlying dark cuticle medially largely obscured by white scales (Figs. 118–136). Lateral margins with white scales large and/or dense. Pronotum widest at base to subequal in width from base to near apex, lateral margins arcuate, more or less parallel or slightly convergent from base to near apex, then variously constricted and more convergent to apex (Figs. 118–136). Pronotal postocular lobes lacking to present and well-developed; postocular vibrissae uniformly short (length less than one-half width of an eye) to long but of unequal length, longest behind base of eye (greatest length greater than one-half width of an eye) (Figs. 137a-156a). *Prosternum.* With shallow, rounded impression anterolaterad of each procoxal cavity; with or without variously developed rounded swelling immediately anterior to each procoxal cavity (Fig. 8). *Legs.* Tarsus moderately broad to broad; articles 2 and 3 more or less subequal in length, width and length of each article subequal to slightly wider than long; article 1 only slightly longer than articles 2 or 3; article 3 moderately deeply bilobed. Ventral tarsal pilosity various in extent from dense and covering almost entire ventral surface of each tarsal article, to lacking entirely from at least more basal articles in few species. Claws connate only at very base to from very base through basal one-third to midlength, not to markedly divergent. Tibia with corbel ridge rounded (Fig. 5). Foretibia with inner margin with small to large denticles in apical one-half to two-thirds; near apex with small, indistinct to moderately large subapical tooth. Metatibia of male with uncus with ventral margin evenly rounded. *Wings.* Absent or present (various in length). *Elytra.* All intervals equally flat except humerus and very base of interval 3 variously swollen and convex. Scale pattern various, more or less vittate (Figs. 131, 133–134, 136) or as marginal band of large white scales (Figs. 118–123). Humeri acute to rounded. *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed to suberect scale-like seta. Female with base of abdominal sternum VII (in some individuals also sterna V and VI) internally (dorsally) with variously developed rounded glabrous shiny median tubercle, evident externally (ventrally) as rounded shallow impression. *Genitalia.* Female. Abdominal sternum VIII with basal arm short to long; lateral arms various in shape (Figs. 157–176). Gonocoxite II elongate triangular in shape; apex not prolonged into marked lobe; stylus moderately large, apical in position (Fig. 117). Spermathecal gland round (Fig. 116). Male. Paired sternite of abdominal sternum VIII lacking distinct basal projections (as in Fig. 97f). Aedeagus moderately robust; in lateral view more or less evenly arcuate throughout length; apex not spatulate (Figs. 177c-196c). Internal sac various, with median dorsal pocket low to high; apical and dorsal median pocket individually distinct or not; various lobes present (Figs. 177a,b-196a,b). Apical sclerite complex present, individual sclerites distinctly scythe-like, simple, lacking median projection.

Comparisons.— *Cleonidius* species will prove most difficult to distinguish from various *Lixus* species. Some Old World species presently regarded as *Lixus*, but not examined by me, may prove to be *Cleonidius*. In North America, north of Mexico, the area where most species of *Cleonidius* are found, no *Lixus* species has a rounded pronotal postocular lobe; at most they possess a variously developed, but usually small, acute postocular projection or else have the anterolateral margin of the pronotum straight to slightly sinuate (Fig. 4). Postocular vibrissae in most New World *Lixus* are of unequal length, long, and have their greatest length behind the base of the eye (Fig. 4). All New World *Lixus* I have examined which possess a variously developed postocular lobe and that have postocular vibrissae of more or less uniform length have the inner margin of the femora variously dentate. Femora are not dentate in any *Cleonidius* species.

Unfortunately there are species of *Cleonidius* which lack or have only slightly developed postocular lobes and have postocular vibrissae as in most *Lixus* species (Figs. 145a, 152a-155a). These can be distinguished from *Lixus* by the relative lengths of the antennal articles, by having a more robust rostrum, and by having the ventral tarsal pilosity variously reduced in extent.

Although there are exceptions (Fig. 141a), world *Lixus* species in general have a very elongate-narrow rostrum (Fig. 4) whereas *Cleonidius* species have a more robust rostrum (Figs. 137a-140a, 142a-156a). Eyes are rounded and slightly convex in many *Lixus*, otherwise are oval to elongate-oval as in all *Cleonidius*. Whereas characters used herein to separate *Lixus* from *Cleonidius* work for the New World fauna, the structural diversity of *Lixus* species in other geographic areas does not permit separation on the basis of these same characters. In the Old World, some *Lixus* species examined are separable from *Cleonidius* species only by lack of the internal tubercle at base of abdominal sternum VII in females, the presence of which is, by definition, universally diagnostic for *Cleonidius*. Such is the situation with *Cylindropterus luxeri* Chevrolat, *Lixus (Lixoglyptus) spartii* Olivier, and *Lixus (Lixoglyptus) circumcinctus* Boheman, the taxa chosen as the out-groups for the phylogenetic analysis of relationships of species of *Cleonidius*.

Apleurus (Gibbostethus) hystrix Fall, because of its more elongate-narrow body form (Fig. 24), may be confused with some *Cleonidius* species, but the tumescent mesosternal process (Fig. 58), robust and deeply punctate rostrum, and prosternal swellings immediately in front of the prosternal impressions (Fig. 7) in the former will readily separate the two.

Checklist of included species.— Nineteen species are recognized in the New World from Nicaragua north to southern Canada. The genus also occurs in the Palearctic Region where it is represented by at least, species formerly placed in the subgenus *Lixestus* Reitter of *Lixus* Fabricius. Of species placed in *Lixestus*, I have examined, and therefore herein include only *Lixus (Lixestus) vibex* (Pallas), the type species of that subgenus by monotypy. Subsequently, aside from species regarded as synonyms of *L. vibex*, Csiki (1934) included *L. pallasi* Faust, originally described as a variation of *L. vibex* and therefore likely a *Cleonidius*, and Ter-Minasyan (1978) further included *L. meles* Boheman. Inclusion of *L. meles* in *Lixestus* by Ter-Minasyan (1978) is supported by Petri (1905) wherein *L. vibex* and *L. meles* key out adjacent to one another. A key to separate the three species included in *Lixestus* is given by Ter-Minasyan (1978).

The twenty species herein placed in *Cleonidius* are as follows:

Cleonidius erysimi species group
    1. *C. erysimi* (Fall)
    2. *C. eustictorrhinus* Anderson
    3. *C. pleuralis* (LeConte)
    4. *C. subcylindricus* Casey
    5. *C. longinasus* Anderson
    6. *C. texanus* (LeConte)
Cleonidius americanus species group
    7. *C. americanus* Csiki
    8. *C. frontalis* (LeConte)
    9. *C. canescens* (LeConte)
    10. *C. infrequens* Anderson

        11. *C. puberulus* (LeConte)
        12. *C. collaris* (LeConte)
        13. *C. notolomus* Anderson
Cleonidius poricollis species group
        14. *C. poricollis* (Mannerheim)
        15. *C. calandroides* (Randall)
   Cleonidius boucardi species group
        16. *C. boucardi* (Chevrolat)
        17. *C. trivittatus* (Say)
        18. *C. placidus* Csiki
        19. *C. quadrilineatus* (Chevrolat)
Incertae sedis
        20. *C. vibex* (Pallas)

Phylogenetic relationships.— See "Phylogenetic analysis" section.

Key to species of adult *Cleonidius*

1   Tarsal claws widely divergent, lacking basal internal flange (as in Fig. 66) . . . . *C. vibex* (Pallas), p. 544

1′   Tarsal claws at most only slightly divergent, basal internal flange well-developed (as in Fig. 67) 2

2 (1′) Head above eye with deep straight sulcus extended posteroventrally from above dorsal margin of eye to area under postocular lobe (Fig. 139). Elytra with apices produced and acuminate (Fig. 120) . . . .
        . . . . *C. pleuralis* (LeConte), p. 504

2′   Head above eye lacking deep straight sulcus. Elytra with apices rounded to at most only slightly acuminate and slightly produced 3

3 (2′) Pronotum extremely irregularly elevated; markedly constricted dorsolaterally near apical margin, deeply and broadly impressed medially at base and longitudinally along lateral margins; with larger punctures on disk very sparse, shallow and indistinct. Metathoracic wings short (approximately equal to one-half length of elytra) . . . .
        . . . . *C. collaris* (LeConte), p. 523

3′   Pronotum more regular in elevation and sculpture; only shallowly to moderately deeply impressed medially at base (also shallowly longitudinally along lateral margins in very few specimens); with larger punctures on disk denser, deeper and more distinct. Metathoracic wings short (approximately equal to or less than one-half length of elytra) to long (approximately equal to or greater than length of elytra) 4

4 (3′) [2] Pronotum with postocular lobes moderately to well-developed and with postocular vibrissae short to moderately long (maximum length equal to or less than one-half width of eye in lateral view) (Figs. 137a-144a,

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[2] An intermediate specimen will key out through both halves of this couplet.

146a-151a). Prosternum in lateral view with anterior flat portion one-third as long as, to approximately equal in length to, more posterior angulate portion (Figs. 137a-144a, 146a-151a) 5

4′ Pronotum with postocular lobes lacking to at most moderately developed and with postocular vibrissae long (maximum length equal to or greater than one-half width of eye in lateral view) (Figs. 145a, 152a-155a). Prosternum in lateral view with anterior flat portion no more than one-half as long as more posterior angulate portion (Fig. 145a, 152a-155a) 19

5 (4) Elytra with sutural intervals lacking scales throughout the greater part of their length, with at most scattered very fine erect hair-like scales (Fig. 118); interval 2 with scales contrastingly dense. . . *C. erysimi* (Fall), p. 500

5′ Elytra with sutural interval with scales uniformly distributed throughout their length (although sparsely so or abraded in some specimens); interval 2 with scales similar in density to those of sutural interval 6

6 (5′) Head behind eye with moderately deep curved sulcus extended posteroventrally from upper one-half of posterior margin of eye to area under postocular lobe (largely covered in many specimens by postocular lobe) (Fig. 150) 7

6′ Head behind eye lacking distinct curved sulcus, with at most one or more wrinkles of cuticle 8

7 (6) Distributed in the northern Atlantic coastal states of the United States and Atlantic coastal provinces of Canada (Fig. 229). Dorsal surface of pronotum and elytra with suberect vestiture short, indistinct. Elytral scale pattern of most specimens not distinctly vittate; scales on interval 2 and intervals 6 to 8 not markedly smaller than scales on adjacent intervals; underlying dark cuticle on interval 2 and intervals 6 to 8 largely obscured by overlying white scales (Fig. 132) . . . . *C. calandroides* (Randall) (in part), p. 531

7′ Distributed in Mexico, and/or Canada and the United States west of 85° W longitude (Fig. 228). Dorsal surface of pronotum and elytra with erect vestiture short to moderately long, distinct. Elytral scale pattern distinctly vittate; scales on interval 2 and intervals 6 to 8 markedly smaller than scales on adjacent intervals; underlying dark cuticle on interval 2 and intervals 6 to 8 not largely obscured by overlying white scales (Fig. 131) . . . . *C. poricollis* (Mannerheim) (in part), p. 527

8 (6′) Elytra distinctly laterally margined with white scales (especially in basal one-half); intervals 9 to 11 with dense moderately elongate broad white scales; otherwise moderately densely uniformly covered with fine white scales smaller than those on intervals 9 to 11 (Figs. 119, 121–123) 9

8′ Elytra not laterally margined, either vittate (Figs. 130–131), more or less uniformly densely scaled (Fig. 129), or mottled with irregularly distributed patches of larger and denser scales (Figs. 124–125); intervals other than 9 to 11 with scales equally large to those on intervals 9 to 11 12

9 (8) Head, pronotum and elytra lacking dorsal erect or suberect vestiture (Fig. 140a). Postocular lobes only moderately developed (Fig. 140a) . . . . *C. subcylindricus* Casey, p. 506

9′   Head, pronotum and elytra with dorsal erect or suberect vestiture short to long (Figs. 138a, 141a-142a). Postocular lobes well-developed (Figs. 138a, 141a-142a) 10

10 (9′) Rostrum with large deep dense punctures; medially longitudinally tumescent and with median carina as fine shiny line at crest of median tumescence; robust (width at apex greater than 0.58 times length) (Fig. 138). . . . . C. eustictorrhinus Anderson, p. 502

10′   Rostrum with small shallow moderately dense punctures; not medially longitudinally tumescent, carina lacking to as variously developed fine shiny line; robust to elongate-narrow (width at apex less than 0.62 times length) (Figs. 141–142). 11

11 (10′) Rostrum (especially in females) very long and narrow (width at apex less than 0.50 times length) (Fig. 141a). Head, pronotum and elytral declivity (and to a lesser extent elytral disk) with dorsal erect vestiture moderately long to very long (lacking from a very few specimens) (Fig. 141a). Associated with Leguminosae . . . . C. longinasus Anderson, p. 508

11′   Rostrum (of both sexes) shorter and more robust (width at apex greater than 0.50 times length) (Fig. 142). Head, pronotum and elytra with dorsal suberect to erect vestiture short to moderately long (Fig. 142a). Associated primarily with Rosaceae and Rhamnaceae, rarely Leguminosae at lower altitudes . . . . C. texanus (LeConte), p. 510

12 (8′) Dorsum (especially of head, pronotum and elytral declivity) with erect vestiture long to very long (Fig. 143a). Rostrum in lateral view with prementum swollen ventrally (Fig. 143a); in dorsal view slightly expanded laterally at midlength (Fig. 143b) . . . . C. americanus Csiki, p. 513

12′   Dorsum with suberect to erect vestiture either lacking or short variously on head, pronotum, and elytra (Figs. 144a, 146a-147a, 149a-152a). Rostrum in lateral view with prementum flat to slightly swollen ventrally (Fig. 144b); in dorsal view not to slightly expanded laterally at midlength (Fig. 144a). 13

13 (12′) Distributed in the northern Atlantic coastal states of the United States and Atlantic coastal provinces of Canada (Fig. 229) . . . . C. calandroides (Randall), p. 531

13′   Distributed in Mexico, and/or Canada and the United States west of 85° W longitude 14

14 (13′) All tarsi with similar and extensive ventral pilose vestiture, articles 1 to 3 with large elongate-oval ventral pilose pads on virtually entire ventral surface of each article (except basal one-third to one-half of article 1) 15

14′   Tarsi with ventral pilose pads small, decreased in extent on more posterior tarsi, either with articles 1 and 2 with small elongate-narrow ventral pilose pads, apical tufts of pilosity, or, with pads lacking; article 3 with moderately large pads not on more than apical two-thirds of ventral surface 16

15 (14) Rostrum not dorsally medially tumescent; base in lateral view appearing continuous with frons (Fig. 152a). Elytra with interval 3 (in some specimens also intervals 4 and 5), and intervals 9 to 11 with dense white

scales, otherwise with scales very sparse or lacking (Fig. 133) . . . .
. . . . *C. boucardi* (Chevrolat) (in part), p. 534

15′   Rostrum dorsally medially longitudinally tumescent; base in lateral view separated from frons by distinct transverse impression (Fig. 150a). Elytra with scales white, fine and sparse, densest on sutural interval, intervals 3 to 7, and 9 to 11 . . . . *C. poricollis* (Mannerheim) (in part), p. 527

16 (14′) Rostrum very short and robust (width at apex greater than 0.70 times length) (Figs. 146–147). 17

16′   Rostrum more elongate-narrow (width at apex less than 0.70 times length) (Figs. 144, 149) 18

17 (16) Rostrum with median carina very distinct, sharp and elevated, also with faint lateral carinae at lateral margins (Fig. 146b); rostrum flat from immediately laterad of median carina to lateral margins; rostrum more or less quadrate in cross-section, lateral margins sharp. Articles of tarsus of hind leg with ventral pilose pads moderately large. Metathoracic wings long (greater than length of elytra) to short (approximately one-half or less than length of elytra) . . . . *C. infrequens* Anderson, p. 520

17   Rostrum with median carina indistinct, low and only slightly elevated, without trace of lateral carinae (Fig. 147b); rostrum declivous from immediately laterad of median carina to lateral margins; rostrum less quadrate in cross-section, the lateral margins rounded. Articles of tarsus of hind leg with ventral pilose pads small. Metathoracic wings short (less than one-half length of elytra) . . . . *C. puberulus* (LeConte), p. 522

18(16′) Elytra elongate compared to pronotal length (LP/LEl less than 0.40) (Fig. 125). Metathoracic wings long (greater than elytra in length). Rostrum more or less circular in cross-section, lateral margins rounded; in dorsal view, slightly swollen laterally at midlength; in lateral view with prementum slightly swollen ventrally. Fore-tibia of most females with inner margin with very large prominent denticles (Fig. 144c) . . . .
. . . . : . . . . *C. frontalis* (LeConte), p. 515

18′   Elytra more robust compared to pronotal length (LP/LEl more than 0.40) (Fig. 130). Metathoracic wings present, varied in length from short (approximately equal to one-half length of elytra) to long (greater than elytra in length). Rostrum more or less quadrate in cross-section, lateral margins sharp; in dorsal view, not swollen laterally at midlength; in lateral view with prementum flat. Fore-tibia of female with inner margin with slightly developed, small denticles . . . . *C. notolomus* Anderson, p. 525

19 (4′) Metathoracic wings short, approximately equal to one-half length of elytra. Eye oval (width greater than 0.60 times length) (Fig. 145a) . . . .
. . . . *C. canescens* (LeConte), p. 518

19′   Metathoracic wings long (approximately equal to or greater than length of elytra). Eye elongate-oval (width less than 0.65 times length) (Figs. 152a-155a) 20

20 (19′) Elytra, except sutural interval and portions of interval 2, uniformly covered with dense white scales (Fig. 135) . . . . *C. placidus* Csiki, p. 539

20′   Elytra distinctly vittate, intervals 6 to 8 with scales lacking or very sparse

compared to intervals 3 to 5 and 9 to 11 (Figs. 133–134, 136) 21

21 (20′) Rostrum not or only slightly dorsally medially tumescent, not distinctly carinate (very slightly so in few specimens) (Fig. 152a). Metatarsus with articles 2 and 3 with ventral pilose pads large, onvirtually entire ventral surface; article 1 with pads elongate-broad, on apical two-thirds of the ventral surface . . . . *C. boucardi* (Chevrolat) (in part), p. 534

21′   Rostrum dorsally medially tumescent, with low rounded carina (Figs. 153a, 155a). Metatarsus with article 3 with ventral pilose pads moderately large, covering the apical one-half to two-thirds of ventral surface; article 2 with pads elongate-narrow, covering the apical two-thirds of the ventral surface; article 1 with pads either present as apical tufts, or elongate and very narrow, covering not more than the apical one-half of the ventral surface 22

22 (21′) Elytra elongate-narrow (width less than 0.55 times length) (Fig. 136). Pronotal disk with moderately long erect hair-like scales (Fig. 155a). Associated primarily with Rosaceae and Rhamnaceae, rarely Leguminosae. . . . . *C. quadrilineatus* (Chevrolat), p. 541

22′   Elytra more robust (width greater than 0.55 times length) (Fig. 134). Pronotal disk with at most short, suberect, indistinct hair-like scales (Fig. 153a). Associated with Leguminosae. . . . . *C. trivittatus* (Say), p. 536

Cleonidius erysimi species group

Diagnosis.— Size small to moderate for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent (Fig. 140a) to present, dense and very long (Fig. 141a). Rostrum very elongate-narrow (Fig. 141a) to moderately robust (Fig. 138a), not to markedly medially tumescent, not to variously carinate; lateral margins rounded. Pronotum with postocular lobes moderately (Fig. 140a) to well-developed (Fig. 141a); postocular vibrissae uniformly short to more or less uniformly moderately long. Elytra with marginal band of scales, only intervals 9 to 11 with white scales large and broad, otherwise with intervals with scales small and fine to absent (Figs. 118–123). Tarsus with ventral pilose vestiture extensive (on almost entire ventral surface of each article) to slightly reduced in extent (on not less than apical one-half of articles 2 and 3). Wings present, length various. Female with abdominal sternum VIII with basal arm short; lateral arms more or less straight and divergent throughout length (Figs. 157–162). Male aedeagus with internal sac with apex of dorsal median pocket rounded (Figs. 177b–182b); lobes B, D, and E absent in some species (Figs. 180a,b–182a,b); dorsal median pocket low to high in lateral view.

Phylogenetic relationships.— The *C. erysimi* group is hypothesized to be sister group to the remainder of North American *Cleonidius* (Figs. 236–237).

Cleonidius erysimi (Fall)
(Figs. 118, 137, 157, 177, 219)

Lixus poricollis; LeConte 1876a,b (misident.). Henshaw 1885 (check., misident.).
Cleonus erysimi Fall 1901:261. Lectotype (here designated), male, one of an undetermined number of syntypes, labelled "'male symbol'", "Redondo/ Cal. 4.7.94.", "Type/ *erysimi*", "M.C.Z./ Type/ 25193", "H.C. FALL/ COLLECTION" and with my designation label "*Cleonus/ erysimi/* Fall LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Redondo, California. Leng 1920 (catal.).
Cleonus (Cleonidius) erysimi; Csiki 1934 (catal.).

Cleonis erysimi; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— This species has infrequently been erroneously referred to as *Lixus poricollis* Mannerheim.

Problems in recognition.— Individuals of this species are easily recognized by the sutural interval of the elytra lacking scales, with at most only scattered very fine erect hair-like scales; interval 2 has scales that are contrastingly dense (Fig. 118). Although some individuals of *C. pleuralis* are superficially similarly patterned, close examination of sutural interval reveals small scales. Regardless, *C. pleuralis* individuals are easily recognized by the deep straight sulcus above each eye (Fig. 139).

Individuals of *C. eustictorrhinus* and *C. texanus*, especially the former, may also prove difficult to separate from those of *C. erysimi* should the elytra be largely abraded of vestiture. *Cleonidius texanus* specimens have a slightly more elongate-narrow rostrum (Fig. 142) and the length of the elytra as compared to the length of the pronotum is greater (see Figs. 197, 200). *Cleonidius eustictorrhinus* and *C. erysimi* individuals will prove most difficult to separate, if abraded, although most *C. erysimi* are brachypterous, whereas all *C. eustictorrhinus* are macropterous.

Description.— *Specimens examined.* 129 males, 179 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 15. *Size.* Length, male, 7.2–11.3 mm; female, 6.1–12.0 mm. Width, male, 2.2–4.1 mm; female, 2.1–4.5 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow to moderately deep punctures, some longitudinally confluent and irregularly impressed immediately above eyes, punctures sparser medially; interspersed with minute punctures. Frons also with moderately dense to dense, elongate-narrow erect hair-like scales immediately above eyes; otherwise with scattered erect hair-like scales and moderately dense to dense, elongate-narrow appressed white scales, sparse to absent medially. Frons separated from base of rostrum by moderately deep to deep transverse impression (Fig. 137a). Base of median tumescence or carina of rostrum with small moderately deep fovea. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum.* Moderately robust, slightly more so in males (width at apex 0.57-0.80 times length) (Fig. 137). In lateral view straight to very slightly curved downward. In dorsal view with postgenae not to very slightly expanded laterally, antennal scrobes very slightly visible. Slightly to markedly medially tumescent from point of antennal insertion to middle of frons (more markedly so basally), with median carina variously developed as rounded to sharp, moderately elevated, fine to broad, glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, small to moderately large, shallow to deep (longitudinally confluent in many specimens), smaller and not longitudinally confluent apically, dorsally interspersed with minute punctures. Dorsally (especially laterally) with sparse to moderately dense, moderately long erect hair-like scales, and laterally with sparse to moderately dense, elongate-narrow white appressed to recumbent scales, medially with vestiture absent to very sparse, appressed, elongate-fine. Epistoma not swollen. *Pronotum.* Median carina variously developed in anterior one-half to three-quarters as slightly to moderately elevated glabrous shiny broad line. Dorsal punctation moderately large to large, moderately dense to dense, deep; smaller and shallower apically; shallower on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, moderately long erect hair-like scales each situated in large puncture (Fig. 137a). Scales dorsally absent along midline, moderately dense, elongate-fine, appressed in pair of paramedian apically slightly narrowed stripes; laterally, absent to very small and sparse. Lateral margins with appressed white scales elongate-fine to elongate-narrow, moderately dense in moderately broad stripe. Flanks with scales smaller and slightly less dense than along lateral margins. Median basal area of disk very shallowly to moderately deeply impressed. Anterolateral margin with pronotal postocular lobes moderately to well-developed; postocular vibrissae short, of uniform length to very slightly longer immediately behind base of eye (approximately one-half width of eye or less) (Fig. 137a). In dorsal view with lateral margins very slightly arcuate and convergent from base to apex; subapical constriction very slight and indistinct. *Prosternum.* With moderately large, moderately deep to deep impression, and moderately to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion, anterior and posterior portions not to slightly differentiated by shallow transverse impression (Fig. 137a). *Elytra.* Elongate-narrow in general form (width at midlength 0.45-0.55 times length in males; 0.48-0.53 in females) (Fig. 118). In dorsal view with lateral margins straight to very slightly arcuate or very slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate, not to slightly divergent. Humerus indistinct, rounded. Dorsally with sparse to moderately dense, suberect to erect, short hair-like scales (abraded in many specimens). Sutural interval with scales lacking throughout greater part of length, with sparse fine scales only at very base; intervals 2 to 7 with scales uniformly moderately dense, various in size from elongate-fine to elongate-narrow on alternate intervals in many specimens; interval 8 with scales absent to very small, fine and sparse; intervals 9 to 11 with scales

uniformly moderately dense to dense, moderately large and elongate-narrow, sparser and smaller apically and at base of interval 11 (Fig. 118). Punctures of elytral striae small, individually distinct, larger and less individually distinct basally, arranged in regular rows. *Wings.* Long (greater than length of elytra [9%, N=29]) to short (less than one-half length of elytra [91%, N=279]). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct to distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third to one-half, not to slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to three-quarters of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical two-thirds to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with sparse to dense appressed elongate-narrow to very elongate-narrow white scales (abraded in part in many specimens). Abdominal sterna III and IV laterally with individually indistinct glabrous patches, each with large puncture and single elongate recumbent to suberect hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with moderately developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-third; markedly inwardly arcuate at apical one-third and convergent to apex, moderately expanded at apex (Fig. 157). Stylus moderately large in length compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 177a,b) elongate and low; median dorsal pocket low, with single elongate moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with small paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe at midlength near dorsal margin (lobe D), with moderately large paired dorsolaterally directed lobe at apical one-third at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired small ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is found from southern British Columbia and Alberta, east to Manitoba, south to southern California, Arizona and extreme western Texas (Fig. 219).

Natural history.— This species is associated with grassland, desert-grassland transitional habitats, Pacific semi-desert, and Great Basin desert. Adults of this species have been collected on a variety of plants (but especially Cruciferae) as follows; *Cleome* sp. (Capparaceae); *Aplopappus ericoides* (Less.) H. and A., *Senecio* sp. (both Compositae); *Brassica* sp., *Brassica oleracea* L. (cabbage), *Dithyrea californica* Harv., *Erysimum* sp., *E. suffrutescens* (Abrams) G. Rossb., *Raphanus sativus* L. (radish), *Stanleya pinnata* (Pursh.) Britton var.*inyoensis* (all Cruciferae); *Adenostoma fasciculatum* H. and A., *Prunus persica* (L.) Batsch. (peach) (Rosaceae). The type series of *Cleonus erysimi* Fall was collected from flowers of *Erysimum capitatum* (Dougl.) Greene on sandhills at Redondo Beach, California (Fall 1901). Adults have been reared from larvae found in crowns of *Lobularia maritima* (L.) Desv. (Cruciferae) at Harris Ranch, Los Alamos, Santa Barbara Co., California.

Adults of the species have been frequently collected in sand dune habitats in coastal California and in other sandy habitats throughout the species range. Adults have been collected throughout the year at altitudes of 15–2359 m (N=40) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. eustictorrhinus*, the two species forming a lineage that is a member of an unresolved trichotomy including *C. pleuralis* and the *C. subcylindricus-C. longinasus-C. texanus* lineage (Fig. 237).

<div align="center">

Cleonidius eustictorrhinus Anderson, new species

(Figs. 119, 138, 158, 178, 216)

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Type Material.— Holotype, male, with a red label "HOLOTYPE", "SACRAMENTO/ CALIF/ XII-13-1949", "D.GIULIANI/ COLLECTOR", "Derham Giuliani/ Collection/ Calif. Acad. Sci./ Accession 1967", "Collection of the/ CALIFORNIA ACADEMY/ OF SCIENCES, San/ Francisco Calif.", "HOLOTYPE *Cleonidius/ eustictorrhinus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CASC). Allotype,

female, with a red label "ALLOTYPE", "Orange Vale/ Sacto.Co./ July 31, 1938/ Quentin Tornich", "ALLOTYPE/ *Cleonidius/ eustictorrhinus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (UCBC, on indefinite loan to CASC). Type locality, Sacramento, California.

Paratypes. 11 males, 12 females. UNITED STATES OF AMERICA: California: Orange Vale, 31.VII.38, Q. Tornish, 1F (UCBC); Lancaster, 19.V.37, E.P. Van Duzee, 1M (CASC); 4mi. w. Meadow Valley, 13.V.49, Middlekauff, 1F (UCBC); Madera County, Bates, 25.III.17, 1F (AMNH); Antioch, 1.IX.37, M. Cazier, 1M (AMNH), 26.IV.68, Monroe, 1F (CWOB); Irvine, Davis, 1M (CNCI); San Diego County, 26.IV.91, Blaisdell, 1M (CASC); Stanford, III.04, 1M (LACM), 11.III.06, 1F (LACM); Fresno County, Waltham Canyon, 26.III.37, Blum, 1F (RSAN); Baldwin Hills, 11.VII.53, Menke, 1F (LACM); Vine Hill, 23.V.65, Johnson, 1F (CWOB); Atascadero, 18.VI.46, Mansfield, 1M (CASC); Laguna Beach, 30.XII.49, 1M (CWOB); Idyllwild, 12.V.34, Stone, 1F (OSUC); Laguna, 20.VI.30, 1F (OSUC), 30.VI.30, 1M (CNCI); Irvine, 1M (RSAN); Yosemite, 17.VI.31, Essig, 1F (UCBC); Stanislaus, XII.35, 1M (CFDA); Carmichael, 17.V.58, Wilkey, 1M (CDFA); Napa County, Pope Valley, 9.V.55, Raven, 1F (CASC).

Derivation of specific epithet.— From the Greek "*eu*" meaning very or exceedingly; "*stiktos*" meaning punctured; and, "*rhinos*" meaning nose. This name is used in reference to the markedly punctured rostrum of members of this species.

Problems in recognition.— Individuals of this species are likely to be confused only with *C. texanus*, *C. subcylindricus*, and *C. erysimi*. Individuals of *C. eustictorrhinus* are easily separated from sympatric individuals of *C. erysimi* by the sutural interval lacking scales in the latter (Fig. 118) and by most *C. erysimi* being brachypterous whereas all *C. eustictorrhinus* are macropterous. Individuals of *C. eustictorrhinus* are easily separated from *C. subcylindricus* by geographic distribution, the former being restricted to California (Fig. 216), the latter to the Atlantic Coastal Plain from Florida north to New York (Fig. 215). *C. subcylindricus* individuals also lack suberect or erect dorsal vestiture (Fig. 140a) whereas *C. eustictorrhinus* have short but distinct erect dorsal vestiture (Fig. 138a). Specimens of *C. eustictorrhinus* will prove most difficult to separate from sympatric individuals of *C. texanus*. In *C. eustictorrhinus* individuals (Fig. 138), the rostrum is medially tumescent, distinctly carinate and has large deep punctures; in *C. texanus* specimens (Fig. 142), the rostrum is not medially tumescent or carinate and has only small shallow punctures. The rostrum is slightly more robust in *C. eustictorrhinus* (Fig. 138) than in *C. texanus* (Fig. 142), *C. eustictorrhinus* tend to be larger than *C. texanus*, and the length of the elytra as compared to the length of the pronotum tends to be greater in *C. texanus* than in *C. eustictorrhinus* (see Figs. 197, 200).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 16. *Size.* Length, male, 8.8–10.4 mm; female, 8.8–11.0 mm. Width, male, 3.2–3.9 mm; female, 3.2–4.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with moderately dense, small to moderately large, shallow punctures; longitudinally confluent and very irregularly impressed immediately above eyes; larger punctures interspersed with sparse minute punctures. Frons also with scales sparse to moderately dense elongate-narrow, erect immediately above eyes; medially and laterally with sparse to moderately dense elongate-narrow appressed to suberect white scales; laterally with moderately dense, short to moderately long fine erect hair-like scales. Frons either continuous with base of rostrum, or slightly separated by shallow transverse impression (Fig. 138a). Base of median tumescence or carina of rostrum with small shallow to moderately deep fovea. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum.* Moderately robust, slightly more so in males (width at apex 0.56-0.69 times length) (Fig. 138). In lateral view slightly curved downward. In dorsal view with postgenae not to slightly laterally expanded, antennal scrobes slightly visible. Moderately to markedly medially tumescent from point of antennal insertion to middle of frons, with median carina variously developed as a rounded, slightly to moderately elevated, broad, glabrous, shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, moderately large to large, shallow to deep (longitudinally confluent in many specimens), smaller and shallower apically, dorsally interspersed with few minute punctures. Dorsally (especially laterally) with sparse to moderately dense, moderately long, suberect to erect hair-like scales, and laterally and medially with sparse to moderately dense, elongate-fine to elongate-narrow, appressed to recumbent, white scales. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half as slightly elevated glabrous narrow to broad line. Dorsal punctation small, dense, shallow; smaller and sparser apically; sparser on flanks; areas between dorsal punctures with dense minute regularly impressed punctures. Dorsally with moderately dense, short erect hair-like scales each situated in larger puncture (Fig. 138a). Scales dorsally absent to sparse, small and fine along midline; moderately dense to dense, elongate-fine, appressed laterad of median line, but not as distinct stripes; laterally, absent to sparse, small and fine. Lateral margins with scales moderately

dense to dense, elongate-narrow to moderately robust, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-fine. Median basal area of disk very shallowly, broadly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short (Fig. 138a). In dorsal view with lateral margins uniformly moderately arcuate and convergent from base to apex; subapical constriction at apical one-fifth indistinct or slight, then straight and convergent to apex (Fig. 119). *Prosternum.* With shallow to moderately deep impression and moderately to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion moderately long, approximately one-half length of posterior more angulate portion; anterior and posterior portions not or slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.49-0.58 times length in males; 0.49-0.55 in females) (Fig. 119). In dorsal view with lateral margins very slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate. Humerus distinct. Dorsally with sparse to moderately dense, suberect to erect, very short to short, hair-like scales. Sutural interval to interval 7 with uniformly moderately dense, fine to elongate-fine, white scales and with scattered patches of larger white scates; interval 8 with scales absent to moderately dense, small and fine basally to elongate-fine apically; intervals 9 to 11 with scales moderately dense to dense, moderately large and elongate-narrow to robust, smaller and finer apically in most specimens (Fig. 119). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, not to slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to three-quarters of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical two-thirds to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with moderately dense to dense elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally with slightly developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-third; markedly abruptly inwardly arcuate at apical one-third; apical one-half to one-third markedly expanded (Fig. 158). Stylus moderately large in length compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 178a,b) elongate and low; median dorsal pocket low, with single elongate moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe near midlength on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired anterodorsolaterally directed lobe at apical one-third at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from California (Fig. 216).

Natural history.— This species is found only in the Pacific semi-desert region. Adults of *C. eustictorrhinus* have been collected only on *Arctostaphylos* sp. (Ericaceae); *Eriogonum* sp. (Polygonaceae); and beans (Leguminosae). Definite host records are not known. Adults have been collected from March to July, and December at altitudes of 9–2002 m (N=8) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. erysimi* (Figs. 236 and 237).

<div style="text-align:center">

Cleonidius pleuralis (LeConte)
(Figs. 120, 139, 159, 179, 217)

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Lixus pleuralis LeConte 1858:78. Holotype (examined), female, labelled with a gold circle (=California), "1062", "Type/ 5177", "*L./ pleuralis/* Lec." (MCZC). Type locality, on Colorado River below the Gila River, California. Gemminger and von Harold 1871 (catal.). LeConte 1876a,b (key, redesc.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889. Horn 1894 (check.).
Lixus californicus; Gemminger and von Harold 1871 (catal.). LeConte 1876a.
Lixus modestus; Gemminger and von Harold 1871 (catal.). LeConte 1876a,b. Henshaw 1885 (check.).
Cleonus (*Cleonidius*) *californicus*; Casey 1891 (as synonym).
Cleonus (*Cleonidius*) *modestus*; Casey 1891 (key). Wickham 1896 (check.). Fall 1901 (check.). Leng 1920 (catal.). Csiki 1934 (catal.). Blackwelder 1947 (check.). Hatch 1971 (key, misident. of *Cleonidius longinasus*).

Cleonus (Cleonidius) pleuralis; Casey 1891 (as synonym). Fall 1901 (check.).
Cleonus modestus; Wickham 1896 (check.). Fall 1901 (check.). Leng 1920 (catal.). Blackwelder 1947 (check.).
Cleonis californicus; O'Brien and Wibmer 1982 (catal., distn., as synonym).
Cleonis modestus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis pleuralis; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Notes about synonymy.— This species has been referred to as *Lixus modestus* Mannerheim
(1843:291) and *L. californicus* Motschulsky (1845:378). The holotype of *Lixus modestus* has
been examined (ZMMU) and as noted elsewhere ("*Nomen dubium*" section) is not a
Cleonidius and is doubtfully a New World *Lixus*. The name *Lixus californicus* Motschulsky is
herein considered a *nomen dubium* and not considered in the nomenclature (see "*Nomen
dubium*" section) of any species of *Cleonidius*.

Problems in recognition.— Adults of this species are very easily recognized by the deep
straight sulcus above each eye (Fig. 139) and the produced and acuminate elytral apices (Fig.
120). Most individuals of *C. poricollis* and some *C. calandroides* possess a shallow curved
sulcus behind the eye (covered by the pronotal postocular lobe in some specimens and difficult
to see) (Fig. 150a), but this should not be confused with the deep straight sulcus in members of
C. pleuralis.

Description.— *Specimens examined.* 89 males, 90 females. Data about variation in LR, WF, WRA, LP, WPB,
WElH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented
in Table 17. *Size.* Length, male, 7.2–10.0 mm; female, 7.3–10.8 mm. Width, male, 2.1–3.1 mm; female, 2.2–3.5 mm.
Head. Eye elongate-oval. Vertex, above eye with deep straight sulcus extended posteriorly from dorsal margin of eye to
area under pronotal postocular lobe. Frons with scattered small shallow punctures and moderately dense minute punctures;
also with moderately dense erect hair-like scales above eyes and moderately dense elongate fine appressed white scales,
slightly sparser medially in most specimens. Frons continuous with base of rostrum, not separated by transverse impression
(Fig. 139a). Most specimens with a shallow median fovea at base of median tumescence or carina of rostrum. Width of
frons greater than or subequal to width at apex of rostrum. *Rostrum.* Elongate-narrow, slightly more so in females (width
at apex 0.44-0.57 times length) (Fig. 139). In lateral view straight to very slightly curved downward. In dorsal view
slightly narrowed apically, postgenae not laterally expanded, antennal scrobes not distinctly visible. Slightly medially
tumescent with median carina in most specimens very low, glabrous shiny line at crest of median tumescence. Dorsal and
lateral punctation sparse, small and shallow, interspersed with moderately dense minute punctures. Dorsally (especially
laterally) with moderately dense erect fine hair-like scales and with moderately dense fine elongate white appressed scales
smaller, finer and sparser apicad of point of antennal insertion. Epistoma not swollen. *Pronotum.* Median carina lacking in
most specimens, indicated in very few specimens by low, glabrous shiny line in anterior one-half. Dorsal and lateral
punctation moderately large, moderately dense, deep; smaller, sparser and shallower apically and medially, the areas
between large dorsal punctures with minute, very shallow punctures. Dorsally with moderately dense, short to moderately
long, fine erect hair-like scales each situated in large puncture (Fig. 139a). Scales dorsally very sparse to absent along
median line, moderately dense, moderately large and elongate in pair of broad paramedian apically slightly narrowed
stripes; laterally, small and fine. Lateral margins with appressed white scales large and elongate-narrow in moderately
broad stripe. Flanks with scales moderately dense, small and fine. Median basal area of disk deeply and broadly impressed.
Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae very short, of uniform length
(Fig. 139a). In dorsal view with lateral margins slightly arcuate and slightly convergent apically from base to more or less
apical one-fifth; gradually to abruptly constricted at apical one-fifth, convergent to apex (Fig. 120). *Prosternum.* With
moderately deep impression, and moderately to well-developed rounded swelling anterior to each procoxal cavity. In lateral
view with anterior flat to slightly angulate portion short, not distinctly differentiated from longer posterior more angulate
portion. *Elytra.* Very elongate-narrow in general form (width at midlength 0.40-0.46 times length in males; 0.39-0.47 in
females) (Fig. 120). In dorsal view with lateral margins straight, subparallel to slightly divergent from apical one-third to
humerus; slightly and evenly arcuate from apical one-third to apex. Elytral apices produced, acuminate and divergent.
Humerus distinct. Dorsally with moderately dense, erect, short to moderately long, fine hair-like scales. Scale pattern
various; sutural interval to interval 8 with uniformly moderately dense, elongate fine appressed white scales to moderately
dense, elongate fine on intervals 2 to 5 and moderately dense but smaller and finer on sutural interval and intervals 6 to 8
(interval 8 with scales very sparse to lacking in some specimens); intervals 9 to 11 with scales more or less uniformly
moderately dense, moderately large and elongate-narrow (Fig. 120). Punctures of elytral striae small, individually distinct,
arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with
small denticles in apical three-quarters; subapical tooth small, indistinct from tibial denticles. Foretibial uncus of both
sexes moderately large, mesotibial and metatibial unci small. Tarsal claws connate in basal one-third to one-half, not
divergent, basal internal flange lacking. Ventral tarsal pilose vestiture of all tarsi of male and female present as
elongate-narrow pads on apical one-half of article 1, as rounded pads on apical one-half of article 2, and as large rounded
pads on apical three-quarters of article 3. *Abdomen.* Ventral surface with moderately dense to dense appressed very

elongate-narrow white scales, sparser along midline. Abdominal sterna III to VI (especially III and IV) with moderately large individually distinct to indistinct glabrous patches, each with large puncture and single elongate appressed to suberect hair-like scale in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly developed, median, shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm very short, indistinct; lateral arms straight and divergent from base to apical one-quarter, markedly inwardly arcuate at apical one-quarter and convergent to apex, slightly expanded at apex (Fig. 159). Stylus moderately large in length compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 179a,b) elongate and low; median dorsal pocket low, with single short broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsally directed lobe at midlength near dorsal margin (lobe D), with moderately large paired dorsolaterally directed lobe at apical one-third at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket truncate in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— Members of this species are found in the southwestern United States of America and adjacent northern Mexico from California, southern Nevada, southern Utah, central New Mexico and extreme western Texas, south to the Mexican border, except in the west where they are found south into Baja California Norte, Mexico (Fig. 217).

Natural history.— This species is associated with desert-grassland transitional habitat, and Chihuahuan, Mojave and Sonoran deserts. Adults of this species have been collected in various sandy habitats such as dunes and dry stream beds or desert washes on *Ephedra californica* Wats. (Ephedraceae); *Chrysothamnus nauseosus* (Pall.) Britton, *C. paniculatus* (Gray) H.M. Hall, *Hymenoclea* sp., *H. salsola* Torr. and Gray, (all Compositae); *Asclepias* sp. (Asclepiadaceae); *Atriplex polycarpa* (Torr.) Wats. (Chenopodiaceae); *Medicago sativa* L. (Leguminosae); and *Brassica*? sp., *Lepidium* sp. (Cruciferae). Definite hosts are not known.

Adults have been collected from February to October at altitudes ranging from -96–1747 m (N=26) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is a member of an unresolved trichotomy that also includes the *C. erysimi-C. eustictorrhinus* lineage and the *C. subcylindricus-C. longinasus-C. texanus* lineage (Fig. 237).

Cleonidius subcylindricus Casey
(Figs. 121, 140, 160, 180, 215)

Cleonus (Cleonidius) subcylindricus Casey 1891:193. Holotype (examined), female, labelled "Fla", "CASEY/ bequest/ 1925", "TYPE USNM/ 37283", "*C.Cl./ subcylindricus/* Cas" (USNM). Type locality, Florida. Csiki 1934 (catal.).

Cleonus (Cleonidius) graniferus Casey 1891:194. NEW SYNONYMY Holotype (examined), female, labelled "Ga.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37284", "*C.Cl./ graniferus/* Cas." (USNM). Type locality, Georgia. Csiki 1934 (catal.).

Lixus lupinus Blatchley 1914:248. Lectotype (designated by Blatchley [1930:38, error as female] examined), male, labelled "TYPE", "Dunedin, Fla./ W.S.B. Coll./ 1.24.1913", "Purdue/ Blatchley/ collection" and with lectotype designation label of Blatchley (Purdue). Type locality, Dunedin, Florida. Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal). Blatchley 1930.

Cleonus subcylindricus; Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.).

Cleonus graniferus; Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.).

Cleonus lupinus; Kingsolver 1972 (synonymy with *Cleonus subcylindricus*).

Cleonis graniferus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis lupinus; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Cleonis subcylindricus; O'Brien and Wibmer 1982 (catal., distn.).

lupinus, incertae sedis; Csiki 1934 (catal.).

Notes about synonymy.— *Cleonus graniferus* Casey is a developmentally abnormal female of *C. subcylindricus* with a short robust rostrum, legs and antennae. Similar developmental abnormalities are also known in other species of *Cleonidius*. *Lixus lupinus* Blatchley was placed in synonymy with *Cleonus subcylindricus* Casey by Kingsolver (1972).

Problems in recognition.— This species is one of only two species of *Cleonidius* found in and restricted to eastern North America (Figs. 215, 229). These two species differ markedly in many structural features and there should be no problem in separating individuals of the two. *C. subcylindricus* individuals are easily distinguished from other members of the *C. texanus* group, with which they may be confused, by the only slightly developed pronotal postocular lobes and by lack of dorsal suberect or erect vestiture (Fig. 140a).

Problems in separation of *C. subcylindricus* from eastern species of *Lixus* are resolved by *Lixus* species, among other characters, lacking broadly rounded pronotal postocular lobes and instead possessing at most a small acute postocular projection and postocular vibrissae that are not more or less uniform in length, but rather variable in length and distinctly longest at some point behind the eye (Fig. 4).

Description.— *Specimens examined.* 11 males, 18 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 18. *Size.* Length, male, 8.9–10.5 mm; female, 8.5–11.3 mm. Width, male, 2.9–3.5 mm; female, 2.8–3.9 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with very dense, small, shallow punctures, some confluent in some specimens. Frons lacking suberect or erect vestiture, with moderately dense, small to moderately large, very fine and elongate appressed white scales (scales abraded medially in most specimens). Frons separated from base of rostrum by shallow transverse impression (Fig. 140a). Base of rostral carina with small shallow fovea. Width of frons less than width at apex of rostrum. *Rostrum.* Moderately robust, very slightly more so in males (width at apex 0.56-0.69 times length) (Fig. 140). In lateral view slightly curved downward. In dorsal view with postgenae slightly expanded laterally, antennal scrobes partially visible. Slightly medially tumescent from point of antennal insertion to base of frons, with distinct, low, glabrous median carina from point of antennal insertion to middle of frons. Dorsal and lateral punctation very dense, small, shallow (many punctures longitudinally confluent in some specimens). Dorsally lacking suberect or erect vestiture; with moderately dense elongate-fine appressed white scales, scales smaller medially. Epistoma slightly elevated and swollen. *Pronotum.* Median carina lacking to variously developed as low, glabrous, shiny line. Dorsal punctation small, dense and shallow; larger and sparser on flanks; areas between larger dorsal punctures with very dense shallow minute punctures, areas between shiny and irregularly elevated. Dorsally lacking suberect or erect vestiture (Fig. 140a). Scales dorsally absent to moderately dense and very small along midline; moderately dense, small and fine, appressed in pair of broad paramedian apically narrowed stripes; laterally absent to moderately dense and very small. Lateral margins with appressed white scales large and robust, moderately dense in a moderately broad stripe. Flanks with scales small and fine. Median basal area of disk very shallowly and very broadly impressed. Anterolateral margin with rounded pronotal postocular lobes moderately developed; postocular vibrissae of approximately uniform length (slightly longer behind basal portion of eye in some specimens with less well-developed postocular lobes). In dorsal view with lateral margins straight, slightly convergent from base to apical one-quarter, then straight and more markedly convergent to apex; subapical constriction indistinct (Fig. 121). *Prosternum.* With shallow to moderately deep transverse impression and with prosternal swelling lacking to slightly developed anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion short, not distinctly differentiated from posterior longer more angulate portion. *Elytra.* Elongate-narrow in general form (width at midlength 0.45-0.50 times length in males; 0.43–0.53 in females) (Fig. 121). In dorsal view with lateral margins subparallel from apical one-third to humerus; moderately evenly arcuate from apical one-third to apex. Elytral apices not produced, sub-acuminate, not divergent. Humerus distinct. Dorsally lacking suberect or erect vestiture. Sutural interval to interval 8 with scales uniformly moderately dense, fine and elongate, white, with scattered patches of slightly larger white scales; intervals 9 to 11 with scales uniformly moderately dense, large, robust and white (Fig. 121). Punctures of elytral striae small, individually distinct, larger and less individually distinct towards base, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct from tibial denticles. Foretibial, mesotibial, and metatibial unci of both sexes moderately large. Tarsal claws connate in basal one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female extensive, present as rounded pads which cover more or less entire ventral surface of all articles, with exception of basal portion of article 1. *Abdomen.* Ventral surface with moderately dense appressed very elongate white scales. Abdominal sterna III and IV (especially laterally), with distinct moderately large glabrous patches, each with large puncture and single elongate appressed scale situated in or near center; lacking suberect or erect vestiture except for small, scattered, sparse hair-like scales on sternum VII of male. Base of abdominal sternum VII of female internally (dorsally) with slightly developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm very short; lateral

arms straight to very slightly sinuate and divergent from base to apex, apices not expanded (Fig. 160). Stylus large in length compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 180a,b) elongate, moderately high; median dorsal pocket moderately high, with single narrow moderately elongate dorsally directed basal lobe (lobe A), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobes B, D, and E lacking. Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is distributed, perhaps discontinuously, along the Atlantic Coastal Plain from New York south to Florida (Fig. 215).

Natural history.— This species is found at various localities on the Atlantic Coastal Plain in the southeastern mesophytic evergreen forest region. This species was described from several specimens collected on flowers of the hoary lupine, *Lupinus diffusus* Nutt. (Leguminosae) near Dunedin, Florida between January 24 and March 18 (Blatchley 1914; Blatchley and Leng 1916). Other adults have been collected in roots of *Lupinus* sp. (Wilmington, North Carolina) and have been reared from *Lupinus cumulicola* Small (Spring Valley, Florida). Adult specimens have been collected from January to May at elevations of sea level to 182 m (N=7) (Fig. 233).

Chorological relationships.— Table V. This species is sympatric with *C. calandroides* in the northern part of its range in New York.

Phylogenetic relationships.— This species is the sister species of the *C. longinasus-C. texanus* lineage (Fig. 237).

Cleonidius longinasus Anderson, new name
(Figs. 122, 141, 161, 181, 214)

Lixus mixtus LeConte 1876a:416 [not Fabricius 1792:417]. Holotype (examined), female, labelled "Col", "B.D.Smith", "Type/ 5178", "*L. mixtus*/ Lec." (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.) Leng 1920 (catal.).
Cleonus (*Cleonidius*) *modestus*; Hatch 1971 (key, redesc., misident.).
Cleonus mixtus; Kingsolver 1972.
Cleonis mixtus; O'Brien and Wibmer 1982 (catal., distn.).
mixtus, incertae sedis; Csiki 1934 (catal.).

Notes about synonymy.— The name *Lixus mixtus* LeConte is a junior homonym and is here replaced with the name *C. longinasus* Anderson.

Derivation of specific epithet.— From the Latin "*longus*" meaning long and "*nasus*" meaning nose. This name is used in reference to the very long rostrum of females of this species (Fig. 141a).

Problems in recognition.— Most individuals, especially females, of this species are easily recognized by the long and narrow rostrum (Fig. 141a). Otherwise, individuals, especially males, are likely only to be confused with *C. eustictorrhinus*, *C. subcylindricus* and *C. texanus*. Individuals of *C. longinasus* are separated from *C. subcylindricus* by the latter entirely lacking suberect or erect dorsal vestiture and being distributed only along the Atlantic Coastal Plain from New York south to Florida. *C. longinasus* and *C. eustictorrhinus* are sympatric in California but individuals are easily distinguished by the more robust, medially tumescent rostrum of the latter (Fig. 138). On the other hand, although most *C. texanus* and *C. longinasus*, where they are sympatric in California and Oregon, can be separated on the basis of the length and width of the rostrum, length of erect dorsal vestiture, and association with different plant taxa, some specimens, especially males, are very difficult to reliably separate as

discussed under the "Problems in recognition" section for *C. texanus*.

A very few individuals of *C. longinasus* have scales on elytral intervals 3 to 5 larger than those on adjacent intervals giving the elytra an indistinctly vittate scale pattern and perhaps resulting in confusion with species with distinctly vittate scale patterns. Specimens from San Francisco, California entirely lack suberect or erect vestiture but have the long narrow rostrum typical of members of this species.

Description.— *Specimens examined.* 44 males, 80 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 19. *Size.* Length, male, 7.2–9.8 mm; female, 6.1–11.2 mm. Width, male, 2.2–3.4 mm; female, 2.1–3–8 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed with minute punctures. Frons also with sparse to moderately dense, elongate-fine to elongate-narrow, white, appressed to suberect scales medially, elongate-narrow and erect immediately above eyes. Some specimens also with moderately dense very elongate-fine erect hair-like scales medially and immediately above eyes. Frons continuous with base of rostrum or only very slightly separated by very shallow indistinct transverse impression (Fig. 141a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Very elongate-narrow, especially so in females (width at apex in male 0.40-0.56 times length; 0.34-0.44 in female) (Fig. 141). In lateral view straight to moderately curved downward (markedly so near apex in some specimens). In dorsal view with postgenae not laterally expanded, antennal scrobes not or only very slightly visible. Rostrum not medially tumescent, with median carina lacking to variously developed as rounded slightly elevated fine glabrous shiny line. Dorsal and lateral punctation dense, small, shallow (longitudinally confluent in many specimens), smaller and not longitudinally confluent apically, dorsally interspersed with minute punctures. Dorsally with suberect or erect vestiture lacking (few specimens) to with sparse to moderately dense, moderately long to very long, erect hair-like scales in basal one-half, erect vestiture lacking from apical one-half; with sparse to moderately dense appressed to suberect elongate-fine scales in basal one-half, lacking from (perhaps abraded) or very sparse in apical one-half in most specimens. Epistoma not swollen. *Pronotum.* Median carina lacking to variously developed in anterior one-half as slightly elevated narrow shiny glabrous line. Dorsal punctation moderately large, moderately dense to dense, moderately deep; smaller and shallower apically; sparser on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally (especially laterally) with sparse to moderately dense, moderately long to very long, erect hair-like scales, each situated in large puncture (Fig. 141a). Scales dorsally absent to moderately dense, small and fine along median line; sparse to dense, elongate-fine to elongate-narrow laterad of median line (forming distinct apically narrowed stripes in many specimens); laterally, absent or sparse to moderately dense, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-narrow. Median basal area of disk broadly and shallowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short. In dorsal view with lateral margins uniformly very slightly arcuate and convergent from base to apex; subapical constriction indistinct. *Prosternum.* With very shallow, indistinct impression and very slightly to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; anterior and posterior portions not to slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.48-0.54 times length in males; 0.48-0.58 in females) (Fig. 122). In dorsal view with lateral margins straight to very slightly arcuate or slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate. Humerus distinct. Dorsally with sparse to moderately dense, short to very long erect hair-like scales (longest and densest on declivity of most specimens; absent on specimens from San Francisco, California). Sutural interval to interval 7 with uniformly moderately dense, fine to elongate-fine scales, scales on intervals 3 to 5 larger than those on sutural interval and interval 2, and intervals 6 and 7 in some specimens; interval 8 with scales small, very fine to fine, sparse to moderately dense; intervals 9 to 11 with scales moderately dense to dense, elongate-narrow to moderately robust, sparser and smaller apically in some specimens (Fig. 122). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-third to one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to two-thirds of article 1, as large oval pads on apical three-quarters to more or less entire ventral surface of article 2, and as large rounded pads on apical three-quarters to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with well-developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-quarter, inwardly arcuate at apical one-quarter and convergent to apex, apices slightly expanded (Fig. 161). Stylus moderately

large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 181a,b) elongate, moderately high; median dorsal pocket moderately high, with single moderately broad elongate dorsally directed basal lobe (lobe A), with large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobes B, D, and E lacking. Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Specimens from San Francisco, California lack dorsal suberect or erect vestiture but are otherwise typical *C. longinasus.* Some specimens from California and Oregon have less elongate-narrow rostra than typical for this species, perhaps due to hydridization with *C. texanus* which in these areas also occurs on Leguminosae. It does not appear to be host plant induced for all *C. longinasus* are found on Leguminosae.

Geographic distribution.— This species is distributed from southern British Columbia and Washington, south to Idaho, western Montana and Wyoming in the east, south to southern California in the west (Fig. 214).

Natural history.— This species is associated with grassland, Pacific semi-desert and Great Basin desert habitats. Adults of this species have only been found associated with Leguminosae. They have been collected on *Lupinus* spp. and *Astragalus* spp. (both Leguminosae) throughout California. No definite host records are known but it is likely that various annual legumes serve as potential host plants throughout the species range. Adults have been collected from February to December at elevations of from 31–2293 m (N = 14) (Fig. 233). Unlike adults of *C. texanus* which are known to occur, albeit rarely, on low altitude Leguminosae, *C. longinasus* are not known from Rosaceae, the presumed primary host of the former species.

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. texanus* (Fig. 237).

Cleonidius texanus (LeConte)
(Figs. 123, 142, 162, 182, 218)

Lixus texanus LeConte 1876a:155. Lectotype (here designated), one of two syntypes, male, labelled with a dark red circle (=Texas), "67", "TYPE/ 5250", "*L.texanus*/ Lec" and with my designation label "*Lixus*/ *texanus* LeC./ LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Texas. LeConte 1876a (in part; misident. of *Cleonidius quadrilineatus*, [mixed type series]). Henshaw 1881–1882 (check.). Henshaw 1885 (check.).
Cleonus (*Cleonidius*) *circumductus* Casey 1891:192. NEW SYNONYMY Holotype (examined), male, labelled "Ari.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37282", "*C.Cl.*/ *circumductus*/ Cas." (USNM). Type locality, Arizona. Csiki 1934 (catal.).
Cleonus (*Cleonidius*) *texanus*; Casey 1891 (key). Csiki 1934 (catal.).
Cleonus circumductus; Wickham 1902 (check.). Leng 1920 (catal.).
Cleonus texanus; Wickham 1902 (check.). Leng 1920 (catal.).
Cleonus canescens; Yothers 1916 (misident.). Essig 1958 (biol., misident.).
Cleonis circumductus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis modestus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).
Cleonis texanus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Casey (1891) distinguished *C. circumductus* Casey from *C. texanus* (LeConte) by the longer, denser and more erect dorsal vestiture. These features of the dorsal vestiture vary throughout the species range and do not warrant separate species status. (See also sections on "Problems in recognition" and "Variation".)

Problems in recognition.— Individuals of this species are likely to be confused only with individuals of *C. longinasus*, *C. eustictorrhinus*, and *C. subcylindricus*. *C. subcylindricus* individuals are easily separated as they lack suberect or erect dorsal vestiture and are found only along the Atlantic Coastal Plain of the eastern United States of America. Separation of *C.*

eustictorrhinus and *C. texanus* individuals is more difficult. Both species occur in California but can be separated by the more robust and medially tumescent rostrum of *C. eustictorrhinus* (Fig. 138) as outlined in the key.

Individuals, especially males, of *C. texanus* and *C. longinasus* are perhaps the most difficult species of *Cleonidius* to reliably separate. Both species are sympatric over a wide geographic range but are especially problematical to distinguish in California and Oregon. Most *C. longinasus* are slightly larger in size, have long to very long dorsal erect vestiture (Fig. 141a), a very elongate-narrow rostrum (especially so in females) (Fig. 141a), and are associated with both low and high altitude Leguminosae. Most *C. texanus* on the other hand have generally shorter dorsal erect vestiture (Fig. 142a), a shorter, slightly more robust rostrum (Fig. 142a), and are associated with Rosaceae or Rhamnaceae. All individuals from Rosaceae or Rhamnaceae are structurally typical *C. texanus*, although not all specimens associated with Leguminosae are *C. longinasus*. I have seen both male and female specimens with short rostra and short dorsal erect vestiture, both character states of *C. texanus*, from low altitude Leguminosae. I consider these as *C. texanus*. Various individuals from the area of sympatry, including some females, but especially males and those individuals lacking data on plant associations, are less easy to separate based on these structural differences. The rostrum in these specimens is generally of a length precluding reliable assignment to either species, however, length of dorsal erect vestiture of many specimens allows for a tentative identification. As a consequence of this variation, some may consider these twoforms as questionably warranting separate species status, but the moderately extensive distribution of *C. longinasus*, yet the lack of *C. longinasus* or *C. texanus* on Leguminosae from areas (particularly Arizona and Texas) where *C. texanus* is found on Rosaceae and Rhamnaceae, and the lack of individuals with structural character states of *C. longinasus* from Rosaceae or Rhamnaceae yet presence of individuals with structural features of *C. texanus* from Leguminosae, argues against conspecificity (the structural differences perhaps induced by association with different host plants). I suspect hybridization to be the likely cause of the complexities in variation but because of the noted assymmetry in plant associations, do not regard it as warranting conspecificity of the two forms.

Description.— *Specimens examined.* 156 males, 174 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 20. *Size.* Length, male, 6.2–8.6 mm; female, 5.3–8.8 mm. Width, male, 1.9–3.2 mm; female, 1.8–3.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed with minute punctures. Frons also with moderately dense, elongate-fine, white appressed to suberect scales medially, elongate-narrow and erect immediately above eyes. Frons continuous with base of rostrum or only very slightly separated by very shallow indistinct transverse impression (Fig. 142a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum.* Elongate-narrow, slightly more so in females (width at apex 0.51–0.68 times length in male; 0.46-0.66 in female) (Fig. 142). In lateral view slightly curved downward (markedly so near apex in some specimens). In dorsal view with postgenae not to very slightly laterally expanded, antennal scrobes only very slightly visible. Rostrum not to very slightly medially tumescent, with median carina lacking. Dorsal and lateral punctation moderately dense to dense, small, shallow (longitudinally confluent in some specimens), smaller and not longitudinally confluent apically, dorsally interspersed with minute punctures. Dorsally with suberect or erect vestiture lacking (few specimens) to with sparse, short, sub-erect to erect hair-like scales laterally and basally, erect vestiture lacking from apical one-half; with sparse to moderately dense recumbent elongate-very-fine to elongate-fine scales laterally in basal one-half, lacking from (perhaps abraded) or very sparse in apical one-half and medially in most specimens. Epistoma not swollen. *Pronotum.* Median carina lacking to variously developed in anterior one-half as indistinct slightly elevated narrow shiny glabrous line. Dorsal punctation moderately large, moderately dense to dense, moderately deep; smaller andshallower apically; sparser on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally (especially laterally) with sparse to moderately dense, short to moderately long, erect hair-like scales, each situated in large puncture (Fig. 142a). Scales dorsally sparse to moderately dense, small and fine along median line; moderately dense, elongate-fine to elongate-narrow laterad of median line; laterally, sparse to

moderately dense, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense, elongate-narrow. Median basal area of disk broadly and shallowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short. In dorsal view with lateral margins uniformly very slightly arcuate and convergent from base to apex; subapical constriction indistinct, or straight and convergent from base to apical one-quarter, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With shallow to moderately deep impression and very slightly to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; anterior and posterior portions not to slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.45-0.51 times length in males; 0.44-0.51 in females) (Fig. 123). In dorsal view with lateral margins straight to very slightly arcuate or slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate. Humerus distinct. Dorsally with sparse to moderately dense, short suberect to erect hair-like scales (longest and densest on declivity of most specimens). Sutural interval to interval 7 with uniformly moderately dense, fine to elongate-fine scales, interval 8 with scales small, very fine to fine, sparse to moderately dense; intervals 9 to 11 with scales moderately dense to dense, elongate-narrow to moderately robust, sparser and smaller apically in some specimens (Fig. 123). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to two-thirds of article 1, as large oval pads on apical three-quarters to more or less entire ventral surface of article 2, and as large rounded pads on apical three-quarters to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with well-developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-third, inwardly arcuate at apical one-third and convergent to apex, apices slightly expanded (Fig. 162). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 182a,b) elongate, moderately high; median dorsal pocket moderately high, with single moderately broad elongate dorsally directed basal lobe (lobe A), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobes B, D, and E lacking. Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation..— None noted, but see "Geographic variation" section for *C. longinasus* and "Problems in recognition" section for *C. texanus.*

Geographic distribution.— This species is distributed from Washington and Idaho, east to Colorado, south to southeastern Texas in the east, and southern California in the west (Fig. 218).

Natural history.— This species is associated with the western xerophytic evergreen forest habitat. Adults have been collected primarily on Rosaceae and Rhamnaceae throughout the species range, but also on Leguminosae, although only in coastal California and Oregon. Records from Rosaceae and Rhamnaceae are primarily at higher altitudes, regardless of geographic location (although especially in oak-piñon-juniper woodlands). Records from Leguminosae are known only from lower altitudes. Adults have been collected on the following plants; *Lupinus* sp. (Leguminosae); *Ceanothus* sp., *C. cuneatus* (Hook.) Nutt., *C. leucodermis* Greene, *C. integerrimus* Hook. and Arn. (Rhamnaceae); *Cercocarpus* sp., *C. ledifolius* Nutt., *C. montanus* Raf., *Cowania mexicana* D. Don., *Prunus amygdalus* Batsch. (almond), *P. persica* Batsch. (peach), *Pyrus communis* L. (pear), *Purshia tridentata* (Pursh.) DC. (all Rosaceae). Adults have been reared only from *Lupinus affinis* J.G. Agardh. (Leguminosae) at Berkeley, California, but I suspect that a variety of Rosaceae and Rhamnaceae serve as hosts at higher altitudes throughout most of the species range. Adults have been collected from January to October at altitudes ranging from 15–2998 m (N = 56) (Fig. 233). Other individuals and I

have collected specimens of *C. texanus* and *C. quadrilineatus* together on various Rosaceae and Rhamnaceae in Arizona and Texas.

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. longinasus* (Fig. 237).

Cleonidius americanus species group

Diagnosis.— Size small to moderate for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent to present, dense, short to very long. Rostrum moderately elongate-narrow (Fig. 143) to very robust (Figs. 146–147), slightly to markedly medially tumescent, not to variously carinate; lateral margins rounded to sharp. Pronotum with postocular lobes absent (Fig. 145) to present and well-developed (Fig. 143); postocular vibrissae uniformly short to long, of unequal length, and longest behind base of eye. Elytra with scale pattern vittate, intervals other than 9 to 11 with white scales equal in size to those on intervals 9 to 11 (Figs. 146,149), or, with scattered patches of large white scales in mottled appearance (Figs. 143–144). Tarsus with ventral pilose vestiture slightly to markedly reduced in extent (on apical one-half to two-thirds of articles 2 and 3) to absent or nearly so on all articles. Wings present, length various. Female with abdominal sternum VIII with basal arm short to long; lateral arms arcuate to more or less straight throughout length. Male with aedeagus with internal sac with apex of dorsal median pocket rounded; lobes A to F present; dorsal median pocket low in lateral view.

Phylogenetic relationships.— Monophyly of this species group is based only on distribution of the apotypic states of extent of ventral tarsal pilosity (homoplasious within *Cleonidius* in species of the *C. boucardi* group). This monophyly is further weakly supported by the tendency for individuals of some species placed in the *C. americanus* group to be brachypterous more so than individuals of species in other groups and to be the only species group whose members may exhibit a mottled elytral scale pattern. These states however cannot be considered synapotypic for they are not shared by all members of the species group and independent evolution of the apotypic state within species of the group is equally parsimonious with consideration of the apotypic state as a groundplan state for the group with subsequent reversions to the plesiotypic state having taken place. The *C. americanus* group is hypothesized to be the sister group to the *C. poricollis* group-*C. boucardi* group lineage, this lineage then sister to the *C. erysimi* group (Figs. 236–237).

Cleonidius americanus Csiki
(Figs. 124, 143, 163, 183, 223)

Cleonus (*Cleonidius*) *sparsus*; Casey 1891 (key, misident.).

Cleonus basalis Fall 1897:242 [not Chevrolat 1860:80]. Holotype (examined), male, labelled "S.Clemente/ Id. CAL./ 5.29.97", "TYPE", "*basalis*/ Fall", "M.C.Z./ Type/ 25192", "H.C. FALL/ COLLECTION" (MCZC). Type locality, San Clemente Island, California.

Cleonus (*Cleonidius*) *americanus* Csiki 1934:64. New name for *Cleonus basalis* Fall. Blackwelder 1939 (check.).

Cleonis americanus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis basalis; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Problems in recognition.— Unabraded specimens of this species should be easily recognized because of the long dorsal erect vestiture (Fig. 143a). Only specimens of *C. longinasus* have equally long erect dorsal vestiture, but they have a different elytral scale pattern and a more elongate-narrow rostrum that is neither laterally expanded at midlength nor with the

prementum swollen ventrally, as in members of *C. americanus* (Fig. 143). Indeed, *C. americanus* and *C. frontalis* are the only species of *Cleonidius* in which the rostrum, in lateral view, has the prementum slightly to markedly swollen ventrally, and in dorsal view is variously expanded laterally at midlength (Figs. 143–144). Abraded specimens throughout the species range in California might therefore only be otherwise confused with *C. frontalis*. From *C. frontalis*, individuals of *C. americanus* can be distinguished by their larger, deeper, and denser dorsal pronotal punctation, absence of large denticles on the inner margin of the fore-tibia of females (Fig. 143c), and the rostrum straight, not slightly curved downward.

Description.— *Specimens examined.* 65 males, 69 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 21. *Size.* Length, male, 4.9–10.9 mm; female, 5.4–11.3 mm. Width, male, 1.9–4.1 mm; female, 2.1–4.1 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed with minute punctures. Frons also with sparse, elongate-fine, white appressed to recumbent scales medially, moderately dense, elongate-narrow and erect immediately above eyes; with dense, very long erect hair-like scales laterally, lacking medially. Frons continuous with base of rostrum or only very slightly separated by shallow transverse impression (Fig. 143a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately elongate-narrow (width at apex 0.51–0.63 times length in males; 0.43–0.59 in females) (Figs. 143a,b). In lateral view straight. In dorsal view with postgenae not to very slightly laterally expanded, antennal scrobes not distinctly visible. Rostrum not to very slightly medially tumescent; slightly laterally expanded at midlength (Fig. 143b); lateral margins more or less rounded, not sharp; with median carina variously developed as moderately elevated broad shiny glabrous line. Dorsal and lateral punctation sparse to moderately dense, small, shallow to deep (longitudinally confluent in many specimens), dorsally interspersed with minute punctures. Dorsally with moderately dense to dense, very long, erect hair-like scales (especially laterally); with moderately dense recumbent elongate-fine scales laterally in basal one-half, lacking from (perhaps abraded) or very sparse in apical one-half and medially in most specimens. Epistoma not swollen. Rostrum in lateral view with submentum slightly to markedly swollen ventrally (Fig. 143a). *Pronotum.* Median carina lacking to variously developed in anterior one-half as low, narrow shiny glabrous line. Dorsal punctation and that of flanks large, dense, deep; smaller, sparser and shallower apically; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, very long, erect hair-like scales, each situated in large puncture (Fig. 143a). Scales dorsally absent to sparse, small and fine along median line; moderately dense, elongate-fine, appressed to recumbent in pair of paramedian slightly apically narrowed stripes; laterally, absent to very sparse, small and fine. Lateral margins with scales moderately dense, elongate-narrow, appressed in narrow stripe. Flanks with scales uniformly moderately dense, elongate-fine. Median basal area of disk broadly and shallowly to moderately deeply impressed. Anterolateral margin with pronotal postocular lobes moderately-developed; postocular vibrissae uniformly short to of unequal length, moderately long and with greatest width approximately one-half width of eye, immediately behind base of eye (Fig. 143a). In dorsal view with lateral margins slightly arcuate and convergent from base to apical one-third, slightly constricted at apical one-third then straight and convergent to apex. *Prosternum.* With small shallow impression and very slightly to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately two-thirds length of posterior more angulate portion; anterior and posterior portions slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.50-0.60 times length in males; 0.50-0.56 in females) (Fig. 124). In dorsal view with lateral margins straight, slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, not divergent. Humerus distinct. Dorsally with moderately dense, moderately long erect hair-like scales. Scales various in color from golden to white; scale pattern various from mottled, with uniformly moderately dense small, fine scales and irregularly distributed patches of denser and larger white scales (Fig. 124); to vittate, with scales uniformly moderately dense, sutural interval and interval 2 (except at base) with golden scales elongate-very-fine, stria 1 with irregularly distributed patches of larger elongate-narrow white scales, base of interval 2 and intervals 3 to 5 with scales elongate-narrow, white, intervals 6 to 11 various from with irregularly distributed patches of denser and larger, elongate-narrow white scales interspersed among elongate-very-fine white or golden scales; to uniformly covered (except intervals 6 and 7 at basal one-third) with large elongate-narrow white scales. Punctures of elytral striae small, individually distinct, larger and less individually distinct basally; arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-narrow pads on apical one-third to one-half of article 1, as elongate-oval pads on apical one-half to two-thirds of article 2, and as large rounded pads on apical two-thirds to more or less entire ventral surface of article 3; of foretarsus of female, as apical tufts to small elongate pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, as moderately large rounded pads on apical two-thirds of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-half of article

1, as elongate-oval pads on apical one-half to two-thirds of article 2, as large rounded pads on apical two-thirds to three-quarters of article 3; of mesotarsus of female, as apical tufts to small elongate pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, as moderately large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male, as elongate-narrow pads on apical one-third to one-half of article 1, as elongate-oval pads on apical one-half to two-thirds of article 2, as large rounded pads on apical two-thirds to three-quarters of article 3; of metatarsus of female, as apical tufts to small elongate pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, as moderately large rounded pads on apical one-half of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large glabrous patches, each with large puncture and single erect very long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with only very slightly developed median shiny tubercle. *Genitalia.* Female (three examined). Abdominal sternum VIII with basal arm short; lateral arms moderately and evenly inwardly arcuate at point slightly beyond midlength, apices slightly expanded (Fig. 163). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 183a,b) elongate and low; median dorsal pocket low, with single elongate narrow dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket truncate in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is found only in California, from the San Francisco Bay region south along the coast and central valleys to the Mexican border (Fig. 223).

Natural history.— This species is found only in the Pacific semi-desert habitat. Adults of this species have been collected on *Artemesia tridentata* Nutt., *Chrysothamnus nauseosus* (Pall.) Britton, *Franseria* sp., *Gutierrezia* sp., and *Aplopappus* sp. (all Compositae). No definite hosts are known but it is probable that a variety of Compositae serve as potential hosts. Adults have been collected from March to November at elevations of from 15–1446 m (N=7) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. frontalis* (Figs. 236 and 237).

Cleonidius frontalis (LeConte)
(Figs. 125, 144, 164, 184, 226)

Cleonus frontalis LeConte 1876a:150. Lectotype (here designated), female, one of three syntypes, labelled with a pale green circle (=Wyoming Territory), "Black Hills/ Hammond", "TYPE/ 5245", "*C. frontalis*/ Lec." and with my designation label "*Cleonus/ frontalis* LeC./ LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Black Hills, South Dakota. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889. Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.). Bleasdell 1937 (check.).

Cleonus sparsus LeConte 1876a:152 [not Zoubkoff 1833:334]. NEW SYNONYMY. Holotype (examined), female, labelled "Col", "*C./ sparsus*/ TYPE Lec.", "Horn Coll/ H8528" and with a red square label (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Leng 1920 (catal.). Essig 1958 (biol., in part misident. of *Cleonidius poricollis*). Arnett *et al.* 1980 (probable misident. of *Cleonidius poricollis*).

Cleonus (*Cleonidius*) *frontalis*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *sparsus*; Casey 1891 (key, misident. of *Cleonidius americanus*). Hatch 1971 (key, redesc., in part misident. of *Cleonidius poricollis*).

Cleonus (*Cleonidius*) *stratus* Csiki 1934:65. NEW SYNONYMY New name for *Cleonus sparsus* LeConte. Blackwelder 1939 (check.).

Cleonis frontalis; O'Brien and Wibmer 1982 (catal., distn., in part misident. of *Cleonidius poricollis* and *Cleonidius puberulus*).

Cleonis sparsus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis stratus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— To initially distinguish *C. sparsus* and *C. frontalis* as separate species, LeConte (1876a) emphasized differences in the extent of ventral pilosity and form of hind tarsal article 3. Variation in these characters is continuous and known to occur in a number of other widespread species, thus I consider these two forms as conspecific. *Cleonidius frontalis* was artibrarily chosen over *C. sparsus* as the valid name for this species.

Casey (1891) incorrectly placed *C. puberulus* as a junior synonym of *C. frontalis* and misidentified individuals of *C. americanus* as *C. sparsus* in his key. Likewise, other authors have frequently confused *C. frontalis*, *C. puberulus*, *C. sparsus*, and less frequently also *C. poricollis*.

Problems in recognition.— Individuals of this species are very likely to be confused with those of *C. americanus*, *C. notolomus* and perhaps, *C. poricollis* and *C. trivittatus*. They are easily separated from *C. americanus* by the long to very long erect dorsal vestiture and dense, large and deep pronotal punctures of the latter. Furthermore, only a few *C. frontalis* are known from California (Fig. 226), whereas *C. americanus* is restricted to that state (Fig. 223). Separation from *C. poricollis* is quite simple as members of that species, where the two are sympatric, possess a curved sulcus behind each eye (Fig. 150a). Similarly, separation from *C. trivittatus* is simple, as individuals of that species lack or at mosthave only very slightly developed postocular lobes (Fig. 153a).

Separation from *C. notolomus* is most difficult and discussed under "Problems in recognition" section for that species.

Most individuals of *Cleonidius* with an elytral scale pattern that is mottled with irregularly distributed patches of larger white scales, and not distinctly vittate (Fig. 125), are this species.

Description.— *Specimens examined.* 121 males, 115 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 22. *Size.* Length, male, 5.7–10.5 mm; female, 5.7–10.8 mm. Width, male, 2.2–3.9 mm; female, 2.2–4.1 mm. *Head.* Eye elongate-oval (Fig. 145a). Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with moderately dense, elongate-narrow, white appressed to recumbent scales medially, moderately dense, elongate-narrow and suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons slightly separated from base of rostrum by shallow to moderately deep transverse impression (Fig. 144a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than, to subequal to, width at apex of rostrum. *Rostrum.* Moderately robust, slightly less so in females (width at apex 0.56-0.71 times length in male; 0.54-0.65 in female) (Figs. 144a,b). In lateral view straight to very slightly curved downward. In dorsal view with postgenae not to very slightly laterally expanded, antenna scrobes very slightly visible. Rostrum slightly to moderately medially tumescent from point of antennal insertion to middle of frons (more markedly so basally); not distinctly to slightly laterally expanded at midlength; lateral margins more or less rounded, not sharp; with median carina absent to variously developed as low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to dense, small, shallow (longitudinally confluent in some specimens); smaller and less dense apically; dorsally interspersed with minute punctures. Dorsally with sparse to moderately dense, short, suberect hair-like scales (especially laterally); with moderately dense appressed elongate-narrow scales laterally in basal one-half, sparse in apical one-half and medially in most specimens. Epistoma not swollen. Rostrum in lateral view with submentum slightly swollen ventrally (Fig. 144a). *Pronotum.* Median carina lacking to variously developed in anterior one-half as low, rounded, moderately broad shiny glabrous line. Dorsal punctation moderately large, moderately dense, moderately deep to deep; smaller, sparser and shallower apically and on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, short to moderately long, suberect to erect hair-like scales, each situated in large puncture (Fig. 144a). Scales dorsally absent to very sparse, small and fine along median line; moderately dense, elongate-fine, appressed in pair of narrow paramedian stripes; laterally, absent to very sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-fine to elongate-narrow, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense, elongate-fine to elongate-narrow. Median basal area of disk broadly and shallowly to moderately deeply impressed. Anterolateral margin with pronotal postocular lobes moderately to well-developed; postocular vibrissae uniformly short (Fig. 144a). In dorsal view with lateral margins slightly to moderately arcuate and slightly convergent from base to apex, or slightly constricted at apical one-third to one-quarter then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and slightly to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long,

approximately two-thirds length of, to slightly shorter than, length of posterior more angulate portion; anterior and posterior portions not to very slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.50-0.56 times length in males; 0.49-0.58 in females) (Fig. 125). In dorsal view with lateral margins straight to very slightly sinuate, slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, not to very slightly divergent. Humerus distinct. Dorsally with sparse, indistinct, very short suberect hair-like scales. Scales various in color from golden to white; scale pattern various with sutural interval and interval 2 with golden to white scales sparse to moderately dense, very small and fine to elongate-fine, intervals 3 to 5 with scales moderately dense, elongate-fine to elongate-narrow, white, intervals 6 to 8 with scales sparse to moderately dense, small and fine to elongate-narrow, white, intervals 9 to 11 with scales moderately dense, elongate-fine to elongate narrow, white; striae of many specimens variously with irregularly distributed patches of larger white scales giving mottled appearance (Fig. 125). Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with very large denticles in apical three-quarters; subapical tooth large, indistinct to distinct from tibial denticles (Fig. 144c). Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-quarter to one-third of article 1, as rounded pads on apical one-third to one-half of article 2, and as large rounded pads on apical one-half to two-thirds of article 3; of foretarsus of female, as apical tufts of article 1, as small rounded pads on apical one-quarter of article 2, as moderately large rounded pads on apical one-half of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-third of article 1, as elongate-oval pads on apical one-third to one-half of article 2, as large rounded pads on apical one-half to two-thirds of article 3; of mesotarsus of female, as apical tufts of article 1, as small elongate-oval pads on apical one-third of article 2, as moderately large rounded pads on apical one-half of article 3; of metatarsus of male, as elongate-narrow pads on apical one-quarter to one-half of article 1, as elongate-narrow pads on apical one-third to one-half of article 2, as elongate-oval to rounded pads on apical one-half to two-thirds of article 3; of metatarsus of female, as elongate-narrow pads on apical one-quarter to one-half of article 1, as elongate-oval pads on apical one-third of article 2, as moderately large rounded pads on apical one-half of article 3. *Abdomen.* Ventral surface with dense, elongate-narrow to broad appressed white scales, sparser and smaller medially on abdominal sterna V to VII. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct large rounded glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with moderately to well-developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms very slightly and evenly inwardly arcuate from base to apical one-quarter, more markedly inwardly arcuate at apical one-quarter and convergent to apex, apices slightly expanded (Fig. 164). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 184a,b) elongate and low; median dorsal pocket low, with single broad short dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket truncate in dorsal view. Apical pocket individually distinct from mediandorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is distributed from southern Alberta east to southern Manitoba, south to California in the west, east to Nebraska, Kansas and western Texas (Fig. 226).

Natural history.— This species is found in grassland, desert-grassland transitional habitats, and Great Basin desert. Very little is known of the natural history of this species despite the large number of specimens collected and examined. Plant associations are very few, the only records known are of adults on *Atriplex* sp., *A. canescens* (Pursh) Nutt., (Chenopodiaceae); and *Melilotus* sp. (Leguminosae). No definite hosts are known. Adults have been collected from January to November, primarily in grassland habitats, at elevations of from 339–3130 m (N=38) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. americanus* (Figs. 236 and 237).

Cleonidius canescens (LeConte)
(Figs. 126, 145, 165, 185, 227)

Cleonus canescens LeConte 1876a:151. Lectotype (here designated), male, one of three syntypes, labelled "Col.", "Type/ 5243", "*C. canescens*/ Lec." and with my designation label "*Cleonus*/ *canescens*/ Lec. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Yothers 1916 (misident. of *Cleonidius texanus*). Leng 1920 (catal.). Essig 1958 (biol., misident. of *Cleonidius texanus*).

Cleonus (*Cleonidius*) *canescens*; Casey 1891 (key).

Cleonus (*Cleonidius*) *grandirostris* Casey 1891:189. Lectotype (here designated), male, one of five syntypes, labelled "N.M.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37278", "*C.Cl.*/ *grandirostris*/ Cas." and with my designation label "*Cleonidius*/ *grandirostris*/ Cas./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, New Mexico. Csiki 1934 (catal.).

Cleonus grandirostris; Wickham 1896 (check.). Fall and Cockerell 1907 (check.). Leng 1920 (catal.).

Cleonus (*Cleonidius*) *coloradensis* Csiki 1934:64. Unjustified replacement name for *Cleonus canescens* LeConte. Blackwelder 1939 (check.).

Cleonis canescens; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis coloradensis; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Cleonis grandirostris; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Notes about synonymy.— O'Brien and Wibmer (1982) synonymized *C. canescens* and *C. grandirostris*. *Cleonus coloradensis* is an unjustified replacement name for *C. canescens*.

Problems in recognition.— This species is easily recognized by the less elongate-oval form of the eye (width greater than 0.60 times length) (Fig. 145a), markedly medially tumescent and robust rostrum (Fig. 145a), anterolateral margin of pronotum lacking postocular lobe (Fig. 145a), and short metathoracic wings.

Description.— *Specimens examined.* 182 males, 216 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 23. *Size.* Length, male, 6.8–8.8 mm; female, 6.9–10.5 mm. Width, male, 2.5–3.7 mm; female, 2.3–4.5 mm. *Head.* Eye more or less oval (width greater than 0.60 times length). Area behind eye with at most only two or three slight wrinkles of cuticle. Frons with moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with dense, elongate-narrow, white suberect scales, slightly smaller medially in some specimens, moderately dense, elongate-narrow and erect immediately above eyes; with moderately dense short suberect hair-like scales. Frons continuous with base of rostrum (Fig. 145a). Base of median tumescence or carina of rostrum (if present) with small, shallow fovea. Width of frons greater than, to subequal to, width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.64-0.84 times length in males; 0.64-0.87 in females) (Fig. 145). In lateral view markedly curved downward. In dorsal view with postgenae moderately laterally expanded, antennal scrobes distinctly visible. Rostrum markedly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins more or less rounded, not sharp; with median carina absent to variously developed as low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense, small, shallow to deep; dorsally interspersed with minute punctures. Dorsally with moderately dense, short, erect hair-like scales (especially laterally); with dense suberect moderately robust scales, smaller and finer apicad of point of antennal insertion. Epistoma moderately transversely swollen at base. *Pronotum.* Median carina lacking to slightly developed in anterior one-half as low, rounded, shiny narrow glabrous line. Dorsal and lateral punctation small to moderately large, moderately dense, shallow to deep; smaller apically; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, very short, fine erect hair-like scales, each situated in large puncture (Fig. 145a). Scales dorsally either uniformly moderately dense medially on disk, or absent along median line; moderately dense, moderately robust, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and fine. Lateral margins with scales moderately dense, moderately robust, appressed. Flanks with scales moderately dense in dorsal one-half, slightly larger in ventral one-half, elongate-fine to elongate-narrow. Median basal area of disk narrowly and moderately deeply impressed. Anterolateral margin with pronotal postocular lobes lacking; postocular vibrissae of unequal length, long, greatest length (approximately two-thirds width of eye) immediately behind base of eye (Fig. 145a). In dorsal view with lateral margins straight to slightly arcuate and slightly convergent from base to apical one-quarter; slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and at most very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion lacking or at most very short and indistinct from posterior more angulate portion. *Elytra.* Moderately robust in general form (width at midlength 0.56-0.62 times length in males; 0.54-0.62 in females) (Fig. 126). In dorsal view with lateral margins very slightly arcuate from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, subacuminate, not divergent. Humerus rounded, indistinct. Dorsally with moderately dense, short suberect hair-like scales.

Scale pattern various; either more or less mottled, with scales moderately dense, small, elongate-narrow to moderately robust on sutural interval and interval 2, moderately dense, large, moderately robust on intervals 3 to 6, moderately dense, large, but with scattered patches of very much smaller scales on intervals 7 to 11 (Fig. 126); or vittate, with scales moderately dense, small and fine on sutural interval and interval 2, moderately dense, uniformly large, moderately robust on intervals 3 to 5, moderately dense, moderately robust, small on intervals 6 and 7, absent to sparse, small, fine on interval 8, uniformly moderately dense, large, moderately robust on intervals 9 to 11. Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings.* Short (approximately equal to one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical two-thirds; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-narrow pads on apical one-quarter of article 1, as elongate-oval pads on apical one-quarter to one-half of article 2, and as large rounded pads on apical two-thirds of article 3; of foretarsus of female, as apical tufts of article 1, as small rounded pads at ventral apex of article 2, as moderately large rounded pads on apical one-half to two-thirds of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-quarter of article 1, as elongate-oval pads on apical one-third of article 2, as large rounded pads on apical one-half to two-thirds of article 3; of mesotarsus of female, as apical tufts of article 1, as small rounded pads at ventral apex of article 2, as moderately large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male, as apical tufts of article 1, as small elongate pads at ventral apex of article 2, as large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of female, as apical tufts of article 1, as small elongate pads at ventral apex of article 2, as moderately large elongate pads on apical one-half to two-thirds of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow appressed white scales, sparser and smaller medially on abdominal sterna V to VII. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct small to large rounded glabrous patches, each with large puncture and single suberect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with at most very slightly-developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm long; lateral arms markedly inwardly arcuate at midlength, apical one-half of each arm laterally expanded (Fig. 165). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 185a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with moderately large median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobe C absent. Apical pocket not distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Elytral and abdominal scale patterns and depth and size of head, rostral and pronotal punctation vary geographically. Specimens from the western part of the species range in Arizona, Utah and Idaho have the vittate form of elytral scale pattern. The ventral surface of the abdomen of these individuals has only small indistinct glabrous patches, and head, rostral and pronotal punctures are small and shallow. Specimens from the rest of the species range to the east have a mottled form of elytral scale pattern (Fig. 126), with ventral abdominal glabrous patches large and distinct, and punctation of the head, rostrum and pronotum slightly larger and deeper.

The rostrum is also more elongate-narrow in the western form than in the eastern form based on measurements of rostral width at apex compared to length of rostrum in both male and female individuals from populations at 6 miles SE. Turkey, Texas; 19 miles SW. Kayenta, Arizona; and Denver, Colorado. Individuals from the population at Denver have the most robust rostra (males, $X=0.805$ $N=8$; females, $X=0.824$ $N=8$), those from 6 mi. SE. Turkey have an intermediate sized rostrum (males, $X=0.780$ $N=8$; females, $X=0.751$ $N=7$), and those from 19 mi. SW Kayenta have the least robust rostrum (males, $X=0.673$ $N=12$; females, $X=0.669$ $N=6$).

Patterns of variation in all characters in this species parallel those in *A. angularis* wherein gene flow appears to be occuring across the continental divide in southern New Mexico and Arizona, but not to the north, in Colorado and Utah.

Geographic distribution.— This species is distributed in the southcentral United States of America from extreme southeastern Idaho east to Nebraska, south in the west to southern

Arizona, east to extreme southern Texas (Fig. 227). There is a questionable record from Lassen National Park in northern California.

Natural history.— This appears to be a species of low to high elevation grassland, desert-grassland transitional, Texas semi-desert, and Great Basin desert habitats. Plant associations are few. Adults have been collected only on *Symphoricarpos* sp. (Caprifoliaceae); *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae); *Medicago sativa* L. (alfalfa) (Leguminosae); and *Mentzelia* sp. (Loasaceae). Definite hosts are not known. Specimens have been collected in all months of the year at elevations of 200–2868 m (N = 56) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister group of the *C. notolomus-C. collaris-C. infrequens-C. puberulus* lineage (Fig. 237).

Cleonidius infrequens Anderson, new species
(Figs. 5, 127, 146, 166, 186, 222)

Type Material.— Holotype, male, with a red label "HOLOTYPE", "Scott City, Kan./5–29–59/H. Willis", "HOLOTYPE/ *Cleonidius*/ *infrequens*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CWOB). Allotype, female, with a red label "ALLOTYPE", "TEX. Muleshoe/Bailey Co./16.IV.1971/G.B. Marshall, "ALLOTYPE/ *Cleonidius*/ *infrequens*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CWOB). Type locality, Scott City, Kansas.

Paratypes. 1 male, 5 females. MEXICO: San Luis Potosi: San Luis Potosi, 17.VI.68, Arsego, 1F (USNM).

UNITED STATES OF AMERICA: New Mexico: Fort Sumner, 19.VIII.51, Robinson, 1M (CWOB); 15mi. n. Las Cruces, 24.VII.79, Richmond, 1F (RSAN). Texas: 4mi. s. Big Springs, 3.VI.72, C.W. O'Brien, 1F (CWOB); D'Hanis, 23.II.63, Fohn, 1F (TAMU); Van Horn, 24.VI.42, Scullen, 1F (OSUC).

Derivation of specific epithet.— From the Latin "*in*" meaning not and "*frequens*" meaning frequent. This name is used in reference to the rarity of individuals of this species.

Problems in recognition.— Individuals of this species are likely to be confused only with those of *C. puberulus* and perhaps also *C. notolomus*. From *C. notolomus*, specimens are easily distinguished by their possession of a more robust, sharply and distinctly medially carinate rostrum, and differently impressed pronotum. Characters allowing for separation of *C. infrequens* from *C. puberulus* are discussed under "Problems in recognition" section for that species.

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 24. *Size*. Length, male, 8.3–8.8 mm; female, 8.2–10.0 mm. Width, male, 3.1–3.3 mm; female, 3.0–3.8 mm. *Head*. Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with moderately dense to dense, elongate-fine to elongate-narrow, white appressed scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons distinctly separated from base of rostrum by deep transverse impression (Fig. 146a). Base of median carina of rostrum with small, shallow fovea. Width of frons less than to subequal to width at apex of rostrum. *Rostrum*. Robust, (width at apex 0.78-0.79 times length in males; 0.75-0.92 in females) (Fig. 146). In lateral view straight to very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins sharp, rostrum flat from immediately laterad of median carina to lateral margins; with median carina present, very distinct, as sharp, elevated, glabrous shiny line at crest of median tumescence; also with indistinct low lateral carina at lateral margin in most specimens (Fig. 146b). Dorsal and lateral punctation moderately dense, moderately large to large, moderately deep and longitudinally confluent (especially so immediately laterad of median carina); dorsally interspersed with sparse minute punctures. Dorsally lacking suberect or erect vestiture; with sparse to moderately dense elongate-narrow to robust appressed white scales. Epistoma transversely swollen at base. *Pronotum*. Median carina lacking to variously developed in anterior one-half as very low, indistinct, broad glabrous line. Dorsal and lateral punctation small to moderately large, moderately dense to dense, moderately deep, not confluent; smaller sparser and shallower apically; areas between large dorsal punctures with minute regularly impressed punctures; punctation sparser and shallower on flanks. Dorsally with moderately dense, short, suberect hair-like scales, each situated in large puncture (Fig. 146a). Scales dorsally absent to sparse, small and fine along median line; dense,

elongate-fine to elongate-narrow, appressed in pair of apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and fine. Lateral margins with scales dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-fine to elongate-narrow. Median basal area of disk broadly and moderately deeply impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, short, greatest length immediately behind base of eye (Fig. 146a). In dorsal view with lateral margins straight and subparallel to slightly and evenly arcuate from base to apical one-third to one-quarter; constricted at apical one-third to one-quarter then straight and convergent to apex. *Prosternum*. With small shallow impression and very slightly to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; posterior and anterior portions not or only slightly separated by shallow transverse impression. *Elytra*. Moderately robust in general form (width at midlength 0.55-0.61 times length in males; 0.52–0.60 in females) (Fig. 127). In dorsal view with lateral margins very slightly sinuate and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, subacuminate, not divergent. Humerus rounded, indistinct. Dorsally with very sparse, irregularly distributed very short suberect hair-like scales; with sutural interval and interval 2 with very sparse to moderately dense, very small and fine to elongate-fine white scales; stria 1 with irregularly distributed patches of larger and denser white scales; intervals 3 to 5 with uniformly dense, elongate-narrow to moderately robust white scales; intervals 6 to 8 with scales absent to very sparse, very small and fine; stria 6 and 7 with irregularly distributed patches of larger and denser white scales; intervals 9 to 11 with scales uniformly dense, white, elongate-narrow to robust (Fig. 127). Punctures of elytral striae small, individually distinct, regular rows. *Wings*. Long (greater than length of elytra [62%, N=5]) to short (approximately equal to one-half length of elytra or less [38%, N=3]). *Legs*. Foretibia of female with inner margin with small to large denticles in apical three-quarters; distinct subapical tooth present. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of both sexes present as elongate pad on apical one-third of article 1, as large rounded pad on apical one-half of article 2 and apical three quarters of article 3; of mesotarsus of both sexes as elongate pad on apical one-quarter to one-third of article 1, as large rounded pad on apical one-half of article 2 and apical three quarters of article 3; and of metatarsus of both sexes as elongate pad on apical one-quarter to one-third of article 1, as small rounded to elongate pad on apical one-half of article 2 and as elongate-oval pad on apical one-half to two-thirds of article 3. *Abdomen*. Ventral surface with moderately dense to dense, elongate-narrow to moderately robust appressed white scales, sparser and smaller medially on abdominal sternum VII of female. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect to erect, short to moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with a slightly-developed median shiny tubercle. *Genitalia*. Female (five examined). Abdominal sternum VIII with basal arm long; lateral arms very slightly inwardly arcuate throughout length, expanded abruptly at apex (Fig. 166). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 186a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— Very few individuals of this species are known from western Kansas, southern New Mexico, and western and central Texas, south to San Luis Potosi, Mexico (Fig. 222).

Natural history.— No definite hosts or host plant associations are known for this species. Adults have been collected in grassland and desert-grassland transitional habitats from February to August at elevations of 873–2242 m (N= 7) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. puberulus* (Figs. 236 and 237).

Cleonidius puberulus (LeConte)
(Figs. 115, 128, 147, 167, 187, 225)

Cleonus puberulus LeConte 1876a:151. Lectotype (here designated), female, one of seven syntypes, labelled "N", "Type/ 5242", "*C. puberulus*/ Lec." and with my designation label "*Cleonus/ puberulus*/ LeC. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Nevada. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Leng 1920 (catal., misinterp. as synonym *Cleonidius frontalis*.
Cleonus (*Cleonidius*) *puberulus*; Casey 1891 (misinterp. as synonym *Cleonidius frontalis*). Csiki 1934 (catal., misinterp. as synonym *Cleonidius frontalis*).
Cleonus (*Cleonidius*) *lobigerinus*; Champion 1902–1906 (in part, distn., misident.).
Cleonis puberulus; O'Brien and Wibmer 1982 (catal., distn., misinterp. as synonym *Cleonidius frontalis*).

Notes about synonymy.— The type locality for this species, given as Nevada (LeConte 1876a), lies outside the geographic range as indicated by specimens I have examined. Perhaps LeConte (1876a) was in error in that the type locality may have been Nebraska, not Nevada (presumably an interpretation made by LeConte based on the "N" on the specimen labels).

Problems in recognition.— Individuals of this species are likely to be confused only with those of *C. infrequens*. Members of both species possess a very broad rostrum not found in other *Cleonidius* species (Figs. 146–147). In *C. infrequens* however, the median rostral carina is sharply elevated and distinct, the lateral margins of the rostrum are sharp, the dorsal surface of the rostrum flat from immediately laterad of the median carina to the lateral margins, the rostral punctures are deep and large, there are very slight low lateral rostral carinae, ventral pilose tarsal vestiture is moderately extensive, and both macropterous and brachypterous forms are known. All of these character states differ from those of *C. puberulus* individuals. Known geographic distributions of the two species (Figs. 222, 225) are allopatric, but there may be sympatry in Colorado or Kansas.

Specimens of *C. puberulus* may also be confused with small *C. poricollis*, *C. notolomus*, and *C. frontalis* but can be distinguished by their more robust rostrum (Fig. 147) and lack of the various diagnostic character states of these other species.

Description.— *Specimens examined.* 10 males, 26 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 25. *Size.* Length, male, 5.1–8.3 mm; female, 6.4–8.4 mm. Width, male, 2.1–3.1 mm; female, 2.6–3.3 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with moderately dense to dense, elongate-fine to elongate-narrow, white appressed scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons separated from base of rostrum by shallow to moderately-deep transverse impression (Fig. 147a). Base of median carina of rostrum with small, shallow fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.71–0.87 times length in males; 0.74-0.82 in females) (Fig. 147). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded, rostrum declivous from immediately laterad of median carina to lateral margins; with median carina present as variously developed slightly elevated, narrow line, more or less obscured in most specimens by overlying scales. Dorsal and lateral punctation moderately dense, small to moderately large, shallow, not longitudinally confluent; dorsally interspersed with dense minute punctures. Dorsally lacking suberect or erect vestiture to with sparse short suberect hair-like scales; moderately dense to dense, elongate-fine to robust appressed white scales. Epistoma transversely swollen at base. *Pronotum.* Median carina lacking to indistinctly developed as very low, broad glabrous line. Dorsal and lateral punctation small, moderately dense to dense, shallow, not confluent; smaller sparser and shallower apically; areas between large dorsal punctures with minute regularly impressed punctures; punctation sparser and shallower on flanks. Dorsally with sparse to moderately dense, very short, suberect hair-like scales, each situated in large puncture (Fig. 147a). Scales dorsally absent to sparse, small and fine along median line; dense, elongate-fine to elongate-narrow, appressed in pair of apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and fine. Lateral margins with scales dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-fine to elongate-narrow. Median basal area of disk broadly and moderately deeply impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, short, greatest length immediately behind base of eye (Fig. 147a). In dorsal view with lateral margins straight and subparallel to slightly and evenly arcuate from base to apical one-third to one-quarter;

constricted at apical one-third to one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and a very slightly developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; posterior and anterior portions separated by shallow to moderately deep transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.53–0.61 times length in males; 0.54-0.60 in females) (Fig. 128). In dorsal view with lateral margins very slightly sinuate and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded to subacuminate, not to very slightly divergent. Humerus rounded, indistinct. Dorsally with sparse to moderately dense, very short suberect hair-like scales; with sutural interval and interval 2 with very sparse to moderately dense, very small and fine to elongate-fine white scales; stria 1 with irregularly distributed patches of larger and denser white scales; intervals 3 to 5 with uniformly dense, elongate-narrow to moderately robust white scales; intervals 6 to 8 with scales absent to dense, very small and fine to moderately robust; stria 6 and 7 with irregularly distributed patches of larger and denser white scales in those specimens with scales of intervals 6 to 8 small and fine; intervals 9 to 11 with scales uniformly dense, white, elongate-narrow to robust (Fig. 148). Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings.* Very short (approximately one-quarter to one-third length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; no distinct subapical tooth present. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, slightly divergent, each with basal internal flange moderately to well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate pad on apical one-quarter to one-third of article 1, as small rounded pad on apical one-half of article 2, and as large round pad on apical two-thirds of article 3; of female as apical tuft of article 1, as small rounded pad on apical one-quarter of article 2, and as large rounded pad on apical one-half of article 3; of mesotarsus of male as apical tuft to small elongate pad on apical one-quarter of article 1, as apical tuft to small elongate pad on apical one-third of article 2, and as small rounded pad on apical one-third of article 3; of female as apical tuft on articles 1 and 2, and as small rounded pad on apical one-third of article 3; of metatarsus of male lacking from, to as small elongate pad on apical one-quarter of article 1, as apical tuft to small elongate pad on apical one-third of article 2, and as small elongate pad on apical one-third of article 3; of female lacking from, to as apical tuft of article 1, as apical tuft of article 2, and a small elongate pad on apical one-quarter of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow to moderately robust appressed white scales, sparser and smaller medially on abdominal sternum VII of female. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect, short hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to moderately developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm moderately long; lateral arms slightly inwardly arcuate at mid-length, very slightly expanded at apex (Fig. 167). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 187a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from extreme southern Alberta and Manitoba, south to southern Wyoming and Colorado (Fig. 225).

Natural history.— A single adult has been collected on *Lesquerella ludoviciana* (Nutt.) Wats. (Cruciferae) in Kansas. Definite hosts are not known. Adults have been collected from April to October in grassland habitats at elevations of 1369–2607 m (N=4) (Fig. 233).

Chorological relationships.— Table V. This species is allopatric with its sister-species *C. infrequens.*

Phylogenetic relationships.— This species is the sister-species of *C. infrequens* (Figs. 236 and 237).

Cleonidius collaris (LeConte)
(Figs. 129, 148, 168, 188, 223)

Cleonus collaris LeConte 1876a:149. Holotype (examined), male, labelled "Col", "*Cleonus/ collaris/* TYPE LeC.", "Horn Coll/ H 8517" and with red square label (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Leng 1920 (catal.).

Cleonus (*Cleonidius*) *collaris*; Casey 1891 (key). Csiki 1934 (catal.).
Cleonis collaris; O'Brien and Wibmer 1982 (catal., distn.).

Problems in recognition.— The markedly irregularly elevated and sculptured pronotum with only sparse shallow and indistinct large punctures is characteristic of members this species and should serve for reliable identification. The pronotum of some specimens of *C. notolomus* is similarly broadly and deeply medially impressed at the base and has shallow longitudinal impressions but is otherwise not as irregularly sculptured as that of *C. collaris*; it also has distinct moderately large, moderately deep dorsal punctation.

Description.— *Specimens examined.* 7 males, 6 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 26. *Size.* Length, male, 8.4–10.4 mm; female, 9.3–10.9 mm. Width, male, 3.3–4.4 mm; female, 4.0–4.6 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with only dense minute punctures. Frons also with dense, moderately robust, pale brownish appressed scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons very slightly separated from base of rostrum by very shallow transverse impression (Fig. 148a). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.61–0.73 times length in male; 0.61–0.69 in female) (Fig. 148). In lateral view very slightly curved downward. In dorsal view with postgenae slightly to moderately laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons (more markedly so basally); not laterally expanded at midlength; lateral margins sharp; with median carina present as variously developed slightly elevated, glabrous, shiny narrow line at crest of median tumescence. Dorsal and lateral punctation sparse, small, shallow, not longitudinally confluent; dorsally interspersed with dense minute punctures. Dorsally lacking suberect or erect vestiture; with dense moderately robust to robust appressed white to pale brown scales. Epistoma moderately transversely swollen at base. *Pronotum.* Extremely irregulary elevated, markedly constricted dorsolaterally at apical one-quarter, deeply and broadly impressed medially at base and longitudinally along lateral margins. Median carina variously developed in anterior one-half from absent to as low, rounded moderately broad glabrous line. Dorsal and lateral punctation and that of flanks small, very sparse, shallow and indistinct; areas between larger dorsal punctures with dense minute regularly impressed punctures. Dorsolaterally with sparse, short, suberect hair-like scales, each situated in large puncture; medially lacking suberect or erect vestiture (Fig. 148a). Scales dorsally absent to sparse, moderately robust along median line; very dense, moderately robust, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales very dense, moderately robust, appressed to recumbent. Flanks with scales dense to very dense, moderately robust, appressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, moderately long, greatest length (approximately one-half width of eye) immediately behind base of eye (Fig. 148a). In dorsal view with lateral margins straight, sinuate or slightly arcuate from base to apical one-quarter; markedly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and slightly developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; posterior and anterior portions slightly to markedly separated by shallow to moderately deep transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.59-0.64 times length in males; 0.60-0.65 in females) (Fig. 129). In dorsal view with lateral margins very slightly and evenly arcuate, sinuate at basal one-quarter and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, not to very slightly divergent. Humerus distinct. Dorsally lacking suberect or erect vestiture; with uniformly dense to very dense, moderately robust appressed white to pale brown scales, absent to sparse and small in scattered patches on striae 1 and 2, and intervals 9 to 11 (Fig. 129). Punctures of elytral striae individually indistinct, obscured by overlying scales. *Wings.* Short (approximately one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; no distinct subapical tooth present. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate pad on apical one-third of article 1, as large rounded pad on apical one-half of article 2, and as large round pad on apical three-quarters of article 3; of female as small elongate pad at apex of article 1, as small rounded pad at apex of article 2, and as large round pad on apical one-half of article 3; of mesotarsus of male as small elongate pad on apical one-quarter to one-third of article 1, as moderately large elongate pad on apical one-third to one-half of article 2, and as large elongate-oval pad on apical two-thirds of article 3; of female as small elongate pad at apex on articles 1 and 2, and as large rounded pad on apical one-half of article 3; of metatarsus of male as small elongate tuft at apex to on apical one-quarter of article 1, as small elongate pad on apical one-third to one-half of article 2, and as large elongate-oval pad on apical one-half of article 3; of female lacking from, to as apical tuft of article 1, as apical tuft on article 2, and as elongate-oval pad on apical one-half of article 3. *Abdomen.* Ventral surface with moderately dense to dense, moderately robust appressed white to pale-brown scales, sparser and smaller medially on abdominal sterna V to VII. Abdominal sterna III to VI (especially III and IV laterally) with individually distinct large rounded glabrous patches, each with large puncture and single recumbent to suberect, moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internal y (dorsally) with markedly developed median shiny tubercle. *Genitalia.* Female (two

examined). Abdominal sternum VIII with basal arm moderately long; lateral arms slightly inwardly arcuate throughout length, very slightly expanded at apex (Fig. 168). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 188a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with small paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket truncate in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from Colorado and adjacent southern Wyoming, western Kansas and northern New Mexico (Fig. 223).

Natural history.— A single adult specimen from Greeley, Colorado was collected on *Lepidium* sp. (pepper-grass; Cruciferae). The very few adults known have been collected in grassland habitats from March to May at elevations of 1697–2608 m (N=3) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. notolomus* (Fig. 237).

Cleonidius notolomus Anderson, new species
(Figs. 130, 149, 169, 189, 225)

Cleonis frontalis; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "Grant Co NM/ X 1932", "RT Kellogg", "HOLOTYPE/ *Cleonidius*/ *notolomus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (USNM). Allotype, female, with a red label "ALLOTYPE", "New Mex: Hidalgo/Co.,1Mi.W.Rodeo/VII-31-1971, J. Doyen & Tschinkel", "J.Doyen Lot/71G20", "ALLOTYPE/ *Cleonidius*/ *notolomus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (UCBC, on indefinite loan to CASC). Type locality, Grant Co., New Mexico.

Paratypes. 15 males, 16 females. MEXICO: Durango: 26mi. w. Durango, 13.VII.75, L.E. Watrous, 1M (CWOB). Mexico: Chapingo, 5.VII.55, Gonzalez, 1F (USNM).

UNITED STATES OF AMERICA: Arizona: Cochise County, Guadalupe Canyon, 31.VII.75, S. McCleve, 1F (SMC); 25mi. n. Douglas, 10.VII.74, S. McCleve, 1M (RSAN); Tucson, XII.27, Downe, 1F (UAT); Cochise, 5.VIII.54, F. Werner, 1F (UAT); Douglas, 23.VIII.27, Jones, 1M (LACM); Chiricahua Mountains, Shake Gulch, 8.VI.68, Menke, 1F (USNM); Sabino Canyon, 2.VII.52, Kelsey, 1F (UAT); Aguirre Lake (10mi. ne. Sasabe), 2.VIII.78, Hetz, 1M (UAT); Hereford, 3.III.41, Jones, 1M (USNM); Green Valley, VII.78, R. Lenczy, iM (USNM); Santa Cruz County, Carmen, 3.VIII.64, Eiland, 1M (USNM); 5mi. s. Cochise, 29.V.61, Statham, 1F (AMNH); Sierra Vista, 4.VIII.79, A.E. Lewis, 1M (CWOB). New Mexico: Grant County, 27.IX.35, Kellogg, 1F (CASC); Silver City, VI.33, Kellogg, 2F (OSUC); White Sands National Monument, Lake Lucero, 2.VIII.74, D. Chandler, 1M (CWOB); White Sands National Monument, R. Lenczy, 1F (USNM), VIII.78, R. Lenczy, 1M (USNM); 5mi. n. Carlsbad, 21.IX.56, MacSwain, 1F (UCBC); Catron County, Quemado, 24.III.64, Hogg, 1F (NMSU). Texas: El Paso, VII, H.F. Wickham, 2M, 4F (USNM); Van Horn, 24.VI.42, Scullen, 1M (OSUC). Utah: Callao, 8.VI.22, Spalding, 1M (USNM).

Derivation of specific epithet.— From the Greek "*notos*" meaning south and "*lomus*" meaning border. This name is used in reference to the distribution of individuals of this species near the southern border of the United States of America.

Problems in recognition.— Adult individuals of this species are most difficult to separate from those of *C. frontalis* . Individuals of both sexes of *C. frontalis* generally have a proportionately longer pronotum compared to elytra (see Fig. 200), more elongate-narrow elytra (see Fig. 197), and more rounded lateral margins of the rostrum. Nearly all *C. frontalis* females are easily distinguished from *C. notolomus* females because the former possess very large denticles along the inner margin of the fore-tibia (Fig. 144c); these denticles are small in all *C. notolomus*. Most *C. frontalis* individuals have the rostrum very slightly laterally swollen at midlength and have the submentum slightly ventrally swollen (Figs. 144a,b); this is not so for *C. notolomus*. All *C. frontalis* are also macropterous, whereas *C. notolomus* are either

macropterous or brachypterous. The two species also are largely allopatric although there is a zone of sympatry in eastern New Mexico and western Texas.

Individuals of *C. notolomus* may also be confused with those of *C. collaris, C. infrequens, C. puberulus, C. poricollis,* and *C. trivittatus. Cleonidius infrequens* and *C. puberulus* individuals are distinguished by their more robust rostra (Figs. 146–147); *C. collaris* by the much more irregularly sculptured and shallowly and indistinctly punctate pronotum, and not distinctly vittate scale pattern; *C. trivittatus* by the at most only slightly developed postocular lobes (Fig. 153a); *C. poricollis* by the curved sulcus behind the eye and the more elongate erect dorsal vestiture (Fig. 150a).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 27. *Size.* Length, male, 7.2–10.8 mm; female, 8.4–11.4 mm. Width, male, 3.0–4.7 mm; female, 3.6–4.7 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small shallow punctures, interspersed with minute punctures. Frons also with moderately dense, elongate-narrow appressed white scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons slightly separated from base of rostrum by shallow transverse impression (Fig. 149a). Base of median carina of rostrum with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.60-0.77 times length in male; 0.59-0.68 in female) (Fig. 149). In lateral view slightly curved downward. In dorsal view with postgenae at most slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins sharp; with median carina as narrow, low, sharp, and distinct shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, small to moderately large, shallow to moderately deep; smaller and less dense apicad of point of antennal insertion; dorsally interspersed with dense minute punctures. Dorsally (especially laterally) with sparse to moderately dense, very short, suberect hair-like scales; also with moderately dense, elongate-narrow, appressed white scales. Epistoma slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from absent to as low, rounded moderately broad glabrous line. Dorsal and lateral punctation small to moderately large, moderately dense, moderately deep, not confluent; smaller, sparser and shallower apically and on flanks; areas between larger dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, short, suberect hair-like scales, each situated in large puncture (Fig. 149a). Scales dorsally absent along median line; dense, elongate-narrow, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales dense, elongate-narrow, appressed to recumbent in moderately broad stripe. Flanks with scales elongate-narrow, slightly less dense than on lateral margins. Median basal portion of disk deeply and broadly impressed; also longitudinally shallowly impressed along lateral margins in most specimens. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, moderately long, greatest length (approximately one-half width of eye) immediately behind base of eye (Fig. 149a). In dorsal view with lateral margins slightly to moderately arcuate and convergent to apex; in some specimens, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and slightly to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to subequal in length to posterior more angulate portion; posterior and anterior portions not or slightly separated by shallow to moderately deep transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.56-0.64 times length in males; 0.58-0.64 in females) (Fig. 130). In dorsal view with lateral margins straight to very slightly sinuate to slightly and evenly arcuate and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, very slightly divergent. Humerus distinct to indistinct. Dorsally with moderately dense, short, suberect to erect hair-like scales; with sutural interval and interval 2 with very sparse to moderately dense, very small and fine to elongate-fine, golden to white scales; intervals 3 to 5 with uniformly dense, elongate-narrow to moderately robust white scales; intervals 6 to 8 with scales lacking to very sparse, very small and very fine, golden to white; intervals 9 to 11 with uniformly dense, elongate-narrow to moderately robust white scales; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales than on adjacent intervals (Fig. 130). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length [21%, N=7]), to short (approximately one-half length of elytra or less [79%, N=26]). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; small subapical tooth present, slightly distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male and female present as elongate-narrow pad on apical one-third to one-half of article 1, as moderately large elongate pad on apical one-third to one-half of article 2, and as large rounded pad on apical two-thirds of article 3; of mesotarsus of male and female as small elongate pad at apex of article 1, as small rounded pad on apical one-quarter to one-third of article 2, and as moderately large rounded pad on apical one-third to one-half of article 3; of metatarsus of male and female as elongate-narrow inner pad on apical one-half and as outer apical tuft of article 1, as elongate-narrow pad on apical one-half of article 2, and as moderately large elongate-oval pad on apical one-half to two-thirds of article 3.

Abdomen. Ventral surface with dense, moderately robust appressed white scales, sparser and smaller medially on abdominal sternum VII of female. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect to erect, short to moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to markedly developed median shiny tubercle. *Genitalia.* Female (five examined). Abdominal sternum VIII with basal arm moderately long; lateral arms slightly to moderately inwardly arcuate at midlength; slightly expanded at apex (Fig. 169). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 189a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with small paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket truncate in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from southeastern Arizona, southern New Mexico, and extreme western Texas, south to central México (Fig. 225).

Natural history.— This species appears to be associated with desert-grassland transitional habitats. There is only a single record of one adult on *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae). No definite hosts are known. Two individuals have been collected at ultraviolet lights. Adults have been collected from March to December at elevations of 870–2161 m (N = 14) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. collaris* (Fig 237).

Cleonidius poricollis species group

Diagnosis.— Size small for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent (Fig. 151a) to present, dense and moderately long (Fig. 150a). Head behind eye with or without variously developed curved sulcus extended from above eye to area under postocular lobe (Fig. 150a). Rostrum moderately robust, moderately to markedly medially tumescent, not to very slightly carinate; lateral margins rounded. Pronotum with postocular lobes well-developed; postocular vibrissae uniformly short (Figs. 150a-151a). Elytra with scale pattern more or less vittate, intervals other than 9 to 11 with white scales equal in size to those on intervals 9 to 11 (Figs. 131–132). Tarsus with ventral pilose vestiture extensive (on greater part of ventral surface of each article) to slightly reduced in extent (on not less than apical one-half of articles 2 and 3). Wings present, of variable length (short in only few specimens). Female with abdominal sternum VIII with basal arm short; lateral arms arcuate (Figs. 170–171). Male with aedeagus with internal sac with apex of dorsal median pocket rounded; lobes A to F present; dorsal median pocket low in lateral view (Figs. 190–191).

Phylogenetic relationships.— Monophyly of this species group is based only on the presence of a curved sulcus behind the eye. The *C. poricollis* group is the sister-group to the *C. boucardi* species group, this lineage sister to the *C. americanus* species group (Fig. 237).

Cleonidius poricollis (Mannerheim)
(Figs. 131, 150, 170, 190, 228)

Cleonis vittatus Kirby 1837:199 [not Zoubkoff 1829:163]. Lectotype (here designated), male, one of two syntypes, labelled "Co-type", "namer", "*Cleonus/ vittatus/* Kirby/ Co-type" and with my designation label "LECTOTYPE/ *Cleonis vittatus/* Kirby desig./ Anderson" (BMNH). Type locality, North America. O'Brien and Wibmer 1982

(catal., distn.).

Lixus poricollis Mannerheim 1843:291. Holotype (examined) female, labelled only with a handwritten label "*poricollis*"/ Escholtz/ Escholtz (ZMMU). Type locality, California. Gemminger and von Harold 1871 (catal.).[3].

Cleonus vittatus; Melsheimer 1853 (check.). Gemminger and von Harold 1871 (catal.). LeConte 1876a (key). Henshaw 1885 (check.). Fall 1901 (check.). Fletcher 1906. Fall and Cockerell 1907 (check.). Gibson 1914. Leng 1920 (catal.).

Cleonus virgatus LeConte 1876a:150 [not Gyllenhal 1834:242]. Holotype (examined), male, labelled "Cal", "*C./ virgatus*/ TYPE Lec.", "Horn Coll/ H8521" and a red square label (MCZC). Type locality, Owen's Valley, California. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889. Leng 1920 (catal., as synonym).

Cleonus (*Cleonidius*) *lobigerinus* Casey 1891:191. Lectotype (here designated), female, one of eight syntypes, labelled "Ari", "CASEY/ bequest/ 1925", "TYPE USNM/ 37281", "*C.Cl./ lobigerinus*/ Cas" and with my designation label "*Cleonus/ lobigerinus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Peach Springs, Arizona. Champion 1902–1906 (in part; distn., misident. of *Cleonidius puberulus*). Csiki 1934 (catal.). Hatch 1971 (key, redesc.).

Cleonus (*Cleonidius*) *kirbyi* Casey 1891:188 (in key). NEW SYNONYMY Holotype (examined), female, labelled "Vic./ Vanc.I.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37299", "*C.Cl./ kirbyi*/ Cas." (USNM). Type locality, Victoria, British Columbia. Csiki 1934 (catal.). Hatch 1971 (key, redesc.).

Cleonus (*Cleonidius*) *poricollis*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *virgatus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *vittatus*; Casey 1891 (key). Hatch 1971 (key, redesc.).

Cleonus lobigerinus; Wickham 1896 (check.). Fall 1901 (check.). Yothers 1916. Leng 1920 (catal.). Tanner 1966 (redesc., biol.).

Cleonus (*Cleonidius*) *boucardi*; Champion 1902–1906 (in part; distn., misident.).

Cleonus kirbyi; Wilcox *et al.*. 1934. Wickham 1902 (check.). Leng 1920 (catal.).

Cleonidius vittatus; Faust 1904 (desig. as type species of *Cleonidius*).

Cleonus quadrilineatus; Anderson 1914 (misident.).

Cleonus poricollis; Leng 1920 (catal.).

Cleonus sparsus; Essig 1958 (in part; biol., misident.). Arnett *et al.* 1980 (probable misident.).

Cleonus (*Cleonidius*) *quadrilineatus*; Hatch 1971 (key, redesc., misident.).

Cleonus (*Cleonidius*) *sparsus*; Hatch 1971 (in part; key, redesc., misident.).

Cleonis frontalis; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Cleonis kirbyi; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis lobigerinus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis poricollis; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis virgatus; O'Brien and Wibmer 1982 (catal., distn.).

vittatus, incertae sedis; Chevrolat 1873.

Notes about synonymy.— There has been much confusion regarding this species and consequently, numerous published misidentifications. *Cleonidius poricollis*, as considered here, includes all those western North American individuals that possess a variously developed, curved sulcus behind each eye (Fig. 150a). Mixed series are however known that include specimens with the sulcus well to only slightly developed, to absent. These sympatric specimens are otherwise indistinguishable and are considered herein to be conspecific. Primary types of *Lixus poricollis* Mannerheim, *Cleonis vittatus* Kirby, *Cleonus virgatus* LeConte, *Cleonus* (*Cleonidius*) *lobigerinus* Casey, and *Cleonus* (*Cleonidius*) *kirbyi* Casey each possess a curved sulcus behind the eye.

Cleonus (*Cleonidius*) *kirbyi* Casey was initially proposed by Casey (1891) as a replacement name for *Cleonus vittatus* LeConte, however LeConte (1876a) did not describe a new species, *Cleonus vittatus*, but rather was referring to *Cleonus vittatus* Kirby contrary to assertions of Casey (1891). Thus *Cleonus* (*Cleonidius*) *kirbyi* Casey should be considered a new species description and not a replacement name. Casey (1891), based only on the brief and inadequate published descriptions of *Cleonis vittatus* Kirby and *Lixus poricollis* Mannerheim, incorrectly considered *Cleonis vittatus* Kirby as a distinct species from *Cleonus vittatus* Kirby, *sensu* LeConte (1876a), but correctly as conspecific with *Cleonus poricollis* (Mannerheim).

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[3]Leconte 1876a,b (misident. *Cleonidius erysimi*). Henshaw 1885 (check., misident. *Cleonidius erysimi*).

Both *Cleonis vittatus* Kirby and *Cleonus virgatus* LeConte are junior homonyms.

Faust (1904) designated *Cleonis vittatus* Kirby as the type species of *Cleonidius*. I have seen a specimen in the British Museum (Natural History), correctly determined by Faust and labelled in his distinctive handwriting.

Problems in recognition.— Most members of this widespread species are easily recognized by the presence of a variously developed (usually deep) curved sulcus behind each eye (Fig. 150a). In many specimens the sulcus is present but largely to completely covered by the postocular lobe. In specimens in which the postocular lobe covers the sulcus, reorientation of the head exposes the sulcus to view. If this is not done, such individuals prove difficult to separate from other species, especially *C. notolomus* and *C. frontalis.* Specimens lacking a sulcus or with only a slightly developed sulcus appear confined to Oregon and British Columbia (perhaps also Washington, although no such specimens have been seen from that area) and are separated from other species of *Cleonidius* by the sparse scales of the elytra (forming a faintly vittate pattern), possession of large pilose ventral tarsal pads, and rostrum with distinct median tumescence, the base of the rostrum distinctly separated from the frons by a transverse impression (Fig. 150a).

The eastern *C. calandroides* is distinguished from the western *C. poricollis* by the short suberect dorsal vestiture (Fig. 151a) and less distinctly vittate elytral scale pattern (intervals 6 to 8 with scales as large as those on intervals 9 to 11) (Fig. 132) in the former. The sulcus is variously developed in individuals of both species but is moderately deep and more distinct in most *C. poricollis* and in only few *C. calandroides.*

Description.— *Specimens examined.* 387 males, 459 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 28. *Size.* Length, male, 4.3–9.3 mm; female, 5.6–10.3 mm. Width, male, 1.8–3.6 mm; female, 2.0–4.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle or with variously developed (moderately deeply in most specimens) curved sulcus extended posteroventrally from upper one-half of posterior margin of eye to area under postocular lobe (sulci continued ventrally and joined at gular suture but covered by prothorax and not visible) (Fig. 150a). Frons with sparse to moderately dense, small shallow punctures, interspersed with minute punctures. Frons also with very sparse to moderately dense, short to moderately long, suberect to erect hair-like scales, moderately dense elongate-fine appressed white scales medially, suberect to erect immediately above eyes. Frons distinctly separated from base of rostrum by moderately deep to deep transverse impression (Fig. 150a). Base of median tumescence of rostrum with small, shallow to moderately deep fovea. Width of frons less than, to subequal to, width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.57-0.71 times length in male; 0.57-0.76 in female) (Fig. 150). In lateral view straight to very slightly curved downward. In dorsal view with postgenae moderately to markedly laterally expanded, antennal scrobes distinctly visible. Rostrum moderately to markedly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, small, shallow (many longitudinally confluent); dorsally interspersed with dense minute punctures. Dorsally with very sparse to moderately dense, short to moderately long, suberect to erect hair-like scales; also with moderately dense, elongate-fine, appressed to recumbent white scales, sparser medially. Epistoma slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from absent to as low, rounded moderately broad glabrous line. Dorsal and lateral punctation moderately large, moderately dense to dense, moderately deep to deep, not confluent; smaller, sparser and shallower apically and on flanks; areas between larger dorsal punctures with or without minute regularly impressed punctures. Dorsally with moderately dense, short to long, erect hair-like scales, each in large puncture (Fig. 150a). Scales dorsally absent to small fine and sparse along median line; moderately dense to dense, elongate-fine to elongate-narrow, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales moderately dense to dense, elongate-fine to elongate-narrow, appressed to recumbent in moderately broad stripe. Flanks with scales elongate-fine to elongate-narrow, sparse to moderately dense. Median basal portion of disk shallowly to deeply and narrowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short (Fig. 150a). In dorsal view with lateral margins slightly arcuate and convergent from base to apical one-quarter, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and moderately to markedly developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately two-thirds to subequal in length to, posterior more angulate portion; posterior and anterior portions not or slightly separated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.50-0.63 times

length in males; 0.50-0.64 in females) (Fig. 131). In dorsal view with lateral margins straight to very slightly sinuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, slightly divergent. Humerus distinct. Dorsally with suberect or erect vestiture lacking to dense, moderately long, erect hair-like scales; with sutural interval with dense, very small and fine to elongate-fine, golden to white scales, interspersed with scattered patches of larger white scales, to with scales uniformly white, dense, small and elongate-fine; intervals 2 with scales golden to white, dense, very small and fine, with scattered patches of larger white scales; intervals 3 to 5 with dense, small and fine to elongate-narrow white scales; intervals 6 to 8 with scales dense, very small and very fine, golden to white, with scattered patches of larger white scales; intervals 9 to 11 with uniformly dense, small to large, elongate-fine to elongate-narrow white scales (Fig. 131). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length [99%, N=838]), to short (approximately one-half length of elytra or less [1%, N=8]). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth indistinct from tibial denticles. Foretibial uncus of both sexes moderately large, mesotibial and metatibial unci small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus, mesotarsus, and metatarsus of male and female present as elongate-oval pad on apical one-half to three-quarters of article 1, as moderately large rounded pad on apical one-half of article 2, and as large round pad on apical three-quarters of article 3 in male, apical one-half to three-quarters in female. *Abdomen.* Ventral surface with moderately dense, elongate-narrow to moderately robust appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect to erect, moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to well-developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms slightly inwardly arcuate throughout length; very slightly expanded at apex (Fig. 170). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 190a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Specimens from coastal localities in Oregon and British Columbia (likely also Washington) differ in a number of respects from individuals from throughout the rest of the species range, exhibiting: generally slightly larger prosternal swellings; generally deeper and denser punctation of head, rostrum and pronotum; smaller elytral scales, the pattern only faintly vittate; lack of sulcus behind the eye; lack of or else very short indistinct dorsal suberect or erect vestiture; and broad foretarsal articles with more extensive ventral pilosity. Not all individuals however possess all of these character states; mixed series are known in which some individuals possess various combinations of the above character states but otherwise possess the typical *C. poricollis* states. As such, no consistent set of character states can be used to justify separation of these Pacific Northwest individuals as a distinct taxonomic entity. A large number of these specimens have been reared from *Erysimum* sp. (wallflower; Cruciferae at Victoria, British Columbia, but other typical *C. poricollis* have also been reared from various Cruciferae throughout the species range. *C. calandroides*, sister-species of *C. poricollis* also occurs on Cruciferae.

Individuals from a series of specimens from San Francisco, California, have the elytra uniformly covered with moderately dense, elongate-fine white scales; the elytra do not appear distinctly vittate. Otherwise these specimens are typical *C. poricollis* and in my view do not warrant separate status.

Geographic distribution.— This is the most widely distributed species of *Cleonidius*, ranging throughout western North America across southern British Columbia, Alberta and Saskatchewan in Canada into the adjacent United States of America east to Michigan in the north, south along the west coast to California in the west and south to western Texas and central México in the east (Fig. 228).

Smith (1957) discusses taxa with populations in prairie habitats in Michigan that are disjunct from populations in the western prairie. The distribution of *C. poricollis* in the northern United States appears to fit this pattern.

Natural history.— This species is associated with a wide variety of habitats: grassland, desert-grassland transitional, Pacific semi-desert, Great Basin desert, Sonoran desert, Mojave desert, and western xerophytic evergreen forest. Adults of this species have been collected on a wide taxonomic range of plants as follows: *Asclepias* sp. (Asclepiadaceae); *Atriplex* sp., *A. nutalli* Wats., *A. rosea* L., *Beta vulgaris* L. (beet), *Eurotia lanata* (Pursh) Moq., *Salsola kali* L. (all Chenopodiaceae); *Ambrosia* sp., *Franseria confertiflora* (DC.) Rydb., *Chrysothamnus* sp., *C. nauseosus* (Pall.) Britton, *C. viscidiflorus* (Hook.) Nutt. var. *typicus*, *Gutierrezia californica* (DC.) Torr. and Gray, *Aplopappus acradenius* (Greene) Blake, *A. venetus* Blake ssp. *vernonioides* (Nutt.) Hall, *Hymenoclea monogyra* T. and G., *Zinnia* sp. (all Compositae); *Sisymbrium altissimum* L., "*S. pestifer*", *Erysimum* sp. (wallflower), *Descurainia sophia* (L.) Webb., *Brassica campestris* L. (mustard), *B. oleracea* L. (broccoli) (all Cruciferae); *Salvia* sp. (Labiatae); *Lupinus* sp., *Trifolium* sp., *Melilotus albus* Desr., *Medicago sativa* L. (all Leguminosae); *Fragaria* sp., *Rubus* sp., *Purshia tridentata* (Pursh) DC. (all Rosaceae). Adults have been reared or collected from the roots of *Chrysothamnus* sp., *Gutierrezia* sp., *G. microcephala* (DC.) Gray, *Aplopappus* sp., *A. venetus* (Hbk.) Blake (all Compositae); *Brassica* sp., *Raphanus sativus* L. (radish), *Erysimum* sp., *Descurainia pinnata* (Walt.) Britton (all Cruciferae). Tanner (1966) reports collection of adults from a *Grayia-Lycium* community, a *Salsola* community, and on *Atriplex canescens* (Pursh) Nutt.. Hatch (1971) notes larvae of this species injuring radishes at Corvallis, Oregon (as *Cleonus sparsus*) and as attacking wallflower roots on a seed farm on Vancouver Island, British Columbia (as *Cleonus kirbyi*).

This species has been collected on various types of vegetation primarily in dry washes and stream beds throughout the species range. Individuals have also been collected on sand dunes or other sandy habitats.

I have seen a single specimen collected from the stomach of *Bufo* sp. (Amphibia).

Adults have been collected from June to November at elevations from sea level to 4004 m (N=132) (Fig. 233).

Chorological relationships.— Table V. *C. poricollis* is allopatric to its sister-species *C. calandroides*.

Phylogenetic relationships.— This species is the sister-species of *C. calandroides*, the only other species in the *C. poricollis* species group (Fig. 236).

<div align="center">

Cleonidius calandroides (Randall)

(Figs. 132, 151, 171, 191, 229)

</div>

Lixus calandroides Randall 1838:42. Type(s) lost. Gemminger and von Harold 1871 (catal.). Sprague and Austin 1875. LeConte 1876a (misinterpret., as synonym of *Lixus musculus*).

Cleonus calandroides; LeConte 1876b (diagnosis). Henshaw 1885 (check.). Casey 1891 (key). Ely 1913 (biol.). Blatchley and Leng 1916 (key, redesc., biol.). Leng 1920 (catal.). Leonard 1926 (check., biol.). Csiki 1934 (catal.). Bruhn 1947 (morphol.). Sanders 1960 (morphol.). Kissinger 1964 (biol.).

Cleonus (*Cleonidius*) *calandroides*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonis calandroides; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— *Lixus calandroides* was described from an unspecified number of specimens from Chelsea Beach, Massachusetts (Randall 1838). Unfortunately type material of Randall has been lost (Sprague and Austin 1875). Following reccomendations of the

International Code of Zoological Nomenclature, no neotype designation is required, because there has been no recent confusion regarding identity of this species. After identification of specimens as this species by Sprague and Austin (1875), LeConte (1876b), based on examination of specimens sent to him by Austin, transferred the species to *Cleonus* and removed the name from his previously proposed synonymy with *Lixus musculus* Say (LeConte 1876a).

Problems in recognition.— This is one of only two species of *Cleonidius* restricted to eastern North America (Figs. 215, 229). These two differ markedly in structural features and should not be confused. The eastern *C. calandroides* is distinguished from the western *C. poricollis* by the short suberect dorsal vestiture (Fig. 151a) and less distinctly vittate elytral scale pattern (intervals 6 to 8 with scales as large as those on intervals 9 to 11) (Fig. 132) in the former. The sulcus behind the eye is variously developed in individuals of both species but is moderately deep and distinct in most *C. poricollis* and in only few *C. calandroides* (see descriptions).

Description.— *Specimens examined.* 65 males, 63 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 29. *Size.* Length, male, 8.0–9.3 mm; female, 5.5–9.6 mm. Width, male, 3.0–3.6 mm; female, 2.1–3.9 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle or with variously developed (moderately deeply in only few specimens) curved sulcus extended posteroventrally from upper one-half of posterior margin of eye to area under postocular lobe (sulci continued ventrally to juncture at gular suture but covered by prothoracic structures and not visible) (as in Fig. 150a). Frons with only scattered small shallow punctures, interspersed with minute punctures. Frons also with moderately dense, short, suberect hair-like scales, sparse to moderately dense elongate-fine appressed white scales medially, suberect to erect immediately above eyes. Frons distinctly separated from base of rostrum by moderately deep to deep transverse impression (Fig. 151a). Base of median tumescence of rostrum with small, shallow to moderately deep fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust, slightly less so in females (width at apex 0.60-0.68 times length in male; 0.56-0.65 in female) (Fig. 151). In lateral view straight to very slightly curved downward. In dorsal view with postgenae moderately laterally expanded, antennal scrobes partially visible. Rostrum medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense, small, shallow (many longitudinally confluent); dorsally interspersed with dense minute punctures. Dorsally with very sparse to moderately dense, short, suberect hair-like scales (especiallly laterally); also with moderately dense, elongate-fine appressed to recumbent white scales, sparser medially. Epistoma slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from absent to as low, rounded narrow glabrous line. Dorsal and lateral punctation moderately large, moderately dense to dense, shallow, not confluent; smaller apically and on flanks; areas between larger dorsal punctures with or without minute regularly impressed punctures. Dorsally with moderately dense, very short, suberect hair-like scales, each situated in large puncture (Fig. 151a). Scales dorsally absent to small fine and sparse along median line; moderately dense, elongate-narrow, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales dense, elongate-fine to elongate-narrow. Median basal portion of disk shallowly to deeply and narrowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short (Fig. 151a). In dorsal view with lateral margins slightly arcuate and slightly convergent from base to apical one-quarter, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and slight to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, subequal in length to posterior more angulate portion; posterior and anterior portions slightly separated by shallow transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.57-0.60 times length in males; 0.55-0.63 in females) (Fig. 132). In dorsal view with lateral margins straight, subparallel to slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, slightly divergent. Humerus distinct. Dorsally with moderately dense, very short, suberect, indistinct hair-like scales; scales more or less uniformly dense, white; with sutural interval and interval 2 with scales small and fine; intervals 3 to 5 and 9 to 11 with scales large and elongate-narrow; scales small and fine to large and elongate-narrow on intervals 6 to 8 (Fig. 132). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, slightly divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus of male present as large pads on more or less entire ventral surface of articles 2 and 3 and apical one-half of article 1; of female, as elongate pad on apical one-half of article 1, as large oval pad on apical three-quarters of article 2, and as large round pad on more or less entire ventral surface of article

3; of mesotarsus of male and female as small elongate-narrow pad on apical one-half of article 1, as large elongate pad on more or less entire ventral surface on articles 2 and 3; of metatarsus of male and female as elongate pad on apical three-quarters of article 1, as large elongate-oval pad on apical one-half of article 2, and as large oval pad on apical three-quarters of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single appressed hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with moderately developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm short; lateral arms slightly inwardly arcuate throughout length; very slightly expanded at apex (Fig. 171). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 191a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is distributed along the northern Atlantic Coast from Long Island, New York, north to New Hampshire and New Brunswick (Fig. 229).

Natural history.— This species breeds in the sea-rocket, *Cakile edentula* (Bigel.) Hook. (Cruciferae). Ely (1913) collected various life stages from larvae to adults in the roots of this plant in mid-August. He reports that larvae live entirely within the root and that the portion of the root living within two or three inches of the surface of the ground is most commonly attacked. Pupation takes place in a coccoon constructed of small shreds of plant material built up in a longitudinal excavation in one side of the root. He further states that the beetles must be very common as virtually all plants examined showed evidence of feeding by larvae. Blatchley and Leng (1916) also state that larvae breed in *Cakile edentula* and other specimens I have examined bear label data indicating they were reared from this plant species. No other plant associations are known. Adults have been collected only on sea beaches from April to October.

Chorological relationships.— Table V. *Cleonidius calandroides* is sympatric only with northern populations of *C. subcylindricus.*

Phylogenetic relationships.— This species is the sister-species of *C. poricollis*, the only other species in the *C. poricollis* species group (Fig. 236).

Cleonidius boucardi species group

Diagnosis.— Size moderately large to large for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent (Fig. 152a) to present, moderately dense and moderately long (Fig. 155a). Rostrum moderately robust, not (Fig. 152a) to moderately (Fig. 155a) medially tumescent, not to variously carinate; lateral margins rounded. Pronotum with postocular lobes absent (Fig. 155a) to very slightly developed (Fig. 152a); postocular vibrissae moderately long to long, of unequal length and longest behind base of eye. Elytra with scale pattern more or less vittate, intervals other than 9 to 11 with white scales equal in size to those on intervals 9 to 11 (Figs. 133–136). Tarsus with ventral pilose vestiture extensive (on greater part of ventral surface of each article) to slightly reduced in extent (on not less than apical one-half of articles 2 and 3). Wings present, long. Female with abdominal sternum VIII with basal arm short to moderate in length; lateral arms arcuate (Figs. 172–175). Male with aedeagus with internal sac with apex of dorsal median pocket variously emarginate or sinuate (Figs. 192a,b-195a,b); lobes A to F present; dorsal median pocket low in lateral view.

Phylogenetic relationships.— Primary characters show this species group to be monophyletic and a member of the unresolved heptachotomy also including the *C. frontalis-C. americanus* lineage, the *C. infrequens-C. puberulus* lineage, *C. canescens*, *C. collaris*, *C. notolomus* (all of the *C. americanus* group), and the *C. poricollis* species group (Fig. 236). Secondary characters further support the monophyly of the group and indicate that the *C. boucardi* group is the sister-group to the *C. poricollis* species group, this lineage sister to the *C. americanus* species group (Fig. 237).

Cleonidius boucardi (Chevrolat)
(Figs. 133, 152, 172, 192, 221)

Apleurus boucardi Chevrolat 1873:79. Holotype (examined), male, labelled "Puebla", "[letter illegible] Boucard", pale blue square label, "Typus", "41", "471/ 85", "Riksmuseum/ Stockholm" and with my label "*Apleurus boucardi/* Chevrolat/ HOLOTYPE/ lab. Anderson" (NRS). Type locality, Puebla, Mexico.
Cleonus carinicollis LeConte 1876a:152 [not Gyllenhal 1834:241]. NEW SYNONYMY. Holotype (examined), female, labelled with a pale green circle (=Wyoming Territory), "Type/ 5241", "C. carinicollis/ Lec." (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.). Brimley 1938 (check.). Arnett *et al.* 1980.
Cleonus (*Cleonidius*) *boucardi*; Casey 1891 (key). Champion 1902–1906 (in part; distn., misident of *Cleonidius poricollis*). Csiki 1934 (catal.).
Cleonus (*Cleonidius*) *carinicollis*; Casey 1891 (key, misident. of *Cleonidius trivittatus* Say).
Cleonus (*Cleonidius*) *lecontei* Casey 1891:190. NEW SYNONYMY Holotype (examined), female, labelled "Ari", "CASEY/ bequest/ 1925", "TYPE USNM/ 37280", "C.Cl./ lecontei/ Cas."(USNM). Type locality, Arizona. Csiki 1934 (catal.).
Cleonus lecontei; Leng 1920 (catal.).
Cleonus (*Cleonidius*) *lecontellus* Csiki 1934:64. NEW SYNONYMY New name for *Cleonus carinicollis* LeConte. Blackwelder 1939 (check.).
Cleonus boucardi; Blackwelder 1947 (check.).
Cleonis boucardi; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis carinicollis; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).
Cleonis lecontei; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis lecontellus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Chevrolat (1873), in describing *C. boucardi* noted the similarity to *C. trivittatus* (Say). Although most individuals of the two species are quite distinct, some individuals are difficult to reliably assign as belonging to either species. One such specimen is the holotype of *Cleonus carinicollis* LeConte, which has dense, extensive ventral tarsal pilose pads, moderately developed postocular lobes (both character states of *C. boucardi*), but also has a rostrum that is medially tumescent and has a low median carina, and an elytral scale pattern which is not that of most *C. boucardi* (the latter, all states of *C. trivittatus*). The type locality is "Colorado Territory" and therefore within the ranges of both species. I have chosen to regard this individual as conspecific with *C. boucardi* and accordingly emphasize the taxonomic significance of the characters of extent of ventral tarsal vestiture and development of postocular lobes as diagnostic for these two species.

Cleonidius lecontellus Csiki is a typical *C. boucardi*, differing from the latter, as noted by Casey (1891), only in details of the elytral scale pattern.

Problems in recognition.— Most individuals of this species are likely to be confused only with *C. trivittatus* and *C. quadrilineatus*. They are however, easily separated by the rostrum not or only slightly dorsally medially tumescent (Fig. 152a), postocular lobes slightly to moderately developed (Fig. 152a), and with all tarsal articles with extensive ventral pilose pads (on more or less entire ventral surface of each article) in *C. boucardi* specimens. In both *C. trivittatus* and *C. quadrilineatus* the rostrum is medially dorsally tumescent and carinate (Figs. 153a, 155a), the postocular lobes are not to moderately developed (but only in few specimens of

C. trivittatus, especially in northern part of the species range in southern Canada) (Figs. 153a, 155a), and the ventral tarsal vestiture is less extensive. A few *C. boucardi* specimens from Kansas and Texas are very similar to *C. trivittatus* in elytral scale pattern and in rostral characters but can be separated by their extensive ventral tarsal pilosity and moderately developed postocular lobes.

Cleonidius boucardi may also be confused with some *C. poricollis* that have a similar faintly vittate elytral scale pattern and lack the curved sulcus behind the eye. Although *C. boucardi* and *C. poricollis* are sympatric over part of their ranges, those individuals of *C. poricollis* that are most likely to be confused with *C. boucardi* are found only in the Pacific Northwest; *C. boucardi* does not occur in this or adjacent areas.

This is the only species of *Cleonidius* that has been extensively collected in Mexico (Fig. 221).

Description.— *Specimens examined.* 73 males, 82 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 30. *Size.* Length, male, 7.5–14.7 mm; female, 8.4–18.6 mm. Width, male, 3.2–5.9 mm; female, 3.4–7.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small to large, shallow to deep punctures, largest, deepest and longitudinally confluent in many specimens immediately above eyes; interspersed with sparse minute punctures. Frons also with sparse, short, suberect hair-like scales, sparse to moderately dense elongate-fine, appressed to recumbent white scales medially, suberect to erect immediately above eyes. Frons continuous with base of rostrum or only very slightly separated from base of rostrum by very shallow transverse impression (Fig. 152a). Base of median tumescence of rostrum with small, shallow to moderately deep fovea. Width of frons subequal to width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.57–0.67 times length in male; 0.59–0.66 in female) (Fig. 152). In lateral view straight to very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes distinctly visible. Rostrum not to very slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow to broad low glabrous shiny line. Dorsal and lateral punctation sparse to dense, smaller to large, moderately deep to deep (dense and large in most specimens with many punctures longitudinally confluent); punctures smaller and shallower apically; dorsally interspersed with dense minute punctures. Dorsally with scattered, short, suberect hair-like scales in some specimens; also with sparse to moderately dense, elongate-fine to elongate-narrow, appressed to recumbent white scales. Epistoma very slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate slightly elevated broad line to elevated sharp narrow glabrous shiny line, well-developed and distinct in most specimens. Dorsal and lateral punctation small, moderately dense, shallow, not confluent; smaller apically and on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Lacking dorsal suberect or erect vestiture (Fig. 152a). Scales dorsally absent in moderately broad median longitudinal line; moderately dense, elongate-fine to elongate-narrow, appressed in pair of narrow to broad apically slightly narrowed paramedian stripes; laterally, scales absent to very sparse, small and fine. Lateral margins with scales moderately dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales sparse to moderately dense, elongate-fine. Median basal portion of disk shallowly to moderately deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes very slightly to moderately developed; postocular vibrissae of unequal length, moderately long to long, greatest length (from one-half to two-thirds width of eye) behind base of eye (Fig. 152a). In dorsal view with lateral margins uniformly slightly arcuate and convergent from base to apex, or slightly constricted at apical one-quarter, then straight and convergent to apex. *Prosternum.* With small very shallow indistinct impression and lacking or with at most only very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion short, approximately equal to one-half length of posterior more angulate portion; posterior and anterior portions not to slightly differentiated by shallow transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.57–0.62 times length in males; 0.54–0.61 in females) (Fig. 133). In dorsal view with lateral margins straight, to very slightly sinuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally lacking suberect or erect dorsal vestiture; sutural interval with moderately dense, small fine white scales; interval 2 with scales absent to sparse small and fine; interval 3 with scales moderately dense large elongate-narrow; intervals 4 and 5 with scales absent to moderately dense, moderately large and elongate-fine; intervals 6 to 8 with scales absent to sparse small and fine; intervals 9 to 11 with scales moderately dense, large elongate-narrow; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales (Fig. 133). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small to large denticles in apical three-quarters; subapical tooth large, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third to one-half, not to slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsal articles present as large pads on more or less entire ventral surface of articles 2 and 3 and apical

one-half to three-quarters of article 1. *Abdomen.* Ventral surface with sparse to moderately dense, elongate-fine to elongate-narrow appressed white scales. Abdominal sterna III to VI lacking glabrous patches or with sterna III and IV with individually indistinct small rounded glabrous patches, each with large puncture and single appressed hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with very slightly developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms moderately inwardly arcuate throughout length; slightly expanded at apex (Fig. 172). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 192a,b) elongate and low; median dorsal pocket low, with single narrow elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired markedly dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with small paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket slightly emarginate medially in dorsal view (Fig. 192b). Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Specimens from Kansas and Texas in the northern part of the species range have a rostrum that is slightly medially tumescent with smaller dorsal punctation, and an elytral scale pattern that is more distinctly vittate.

Geographic distribution.— This species is found from extreme southern California and Arizona in the west, and Kansas and northern Texas in the east, south through central México to Honduras (Fig. 221).

Natural history.— This species lives in mesquite-grassland and grassland habitat throughout Mexico and the southern United States. Plant associations are not known for adults of this species, which have been collected from March to September at elevations of 255–3385 m (N = 29) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of the *C. trivittatus-C. quadrilineatus-C. placidus* lineage in the *C. boucardi* group (Fig. 237).

Cleonidius trivittatus (Say)
(Figs. 134, 153, 173, 193, 220)

Cleonus trivittatus Say 1831:10. Neotype (here designated, from the LeConte Collection), female, labelled with a pale green circle (= Wyoming Territory), "1847", "J. LECONTE/ COLLECTION", "*Cl./ trivittatus/* Say" and with my designation label "*Cleonus trivittatus/* Say NEOTYPE/ desig. Anderson" (MCZC). Type locality, Colorado. Melsheimer 1853 (check.). LeConte 1859b (error as *C. vittatus* Say). Gemminger and von Harold 1871 (catal.). LeConte 1876a (key). Henshaw 1885 (check.). Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Leng 1920 (catal.). Blackwelder 1947 (check.). Essig 1958 (biol.). Kumar *et al.* 1976 (in part; biol.).

Rhynchophorus praepotens Say 1831:21. Type destroyed.

Lixus praepotens; Boheman 1836 (redescr.).

Apleurus trivittatus; Chevrolat 1873.

Cleonus inornatus LeConte 1876a:149. NEW SYNONYMY Holotype (examined), female, labelled "Cal", "*C./ inornatus/* TYPE LeC", "Horn Coll/ H 8519" (MCZC). Type locality, Owen's Valley, California. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Fall 1901 (check.). Leng 1920 (catal.).

Cleonus (*Cleonidius*) *bicarinatus* Casey 1891:190 [not Gebler 1830:158]. NEW SYNONYMY Holotype (examined), male, labelled "Tex", "CASEY/ bequest/ 1925", "TYPE USNM/ 37279", "*C.Cl./ bicarinatus/* Cas" (USNM). Type locality, near Austin, Texas. Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *carinicollis*; Casey 1891 (key, misident.).

Cleonus (*Cleonidius*) *inornatus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *praepotens*; Casey 1891 (as synonym).

Cleonus (*Cleonidius*) *trivittatus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus bicarinatus; Leng 1920 (catal.).

Cleonus quadrilineatus; Pierce 1907 (biol., misident.). Chittenden 1911 (biol., misident.). Blatchley and Leng 1916 (figure, misident.). Yothers 1916 (misident., in part). Essig 1958 (biol., misident.). Arnett *et al.* 1980 (key, redesc., biol., misident.).

Cleonis bicarinatus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis inornatus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis praepotens; O'Brien and Wibmer 1982 (catal., distn. as synonym).
Cleonis trivittatus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— The type series of this species has been lost. I have selected and designated as neotype, a specimen from the LeConte collection, because it is generally considered that LeConte compared his material with that of Say before the loss of the latter. This collection thus represents one of the best sources of reliably identified specimens of Say species. The type locality of the original type series is given as "Arkansaw" (Say 1831) but it is later stated that he (Say) "obtained two or three specimens near the Rocky Mountains". The neotype selected is from "Colorado Territory" which probably refers to the same general area as that intended by the use of "Arkansaw" by Say (1831), which, as indicated by the reference to the Rocky Mountains, undoubtedly refers to more than what is presently the state of Arkansas.

Rhynchophorus praepotens Say (type lost) was regarded by LeConte (1859b) as conspecific with *Cleonus trivittatus* Say. This synonymy has since been generally followed and thus no neotype designation is required. LeConte (1859b) also states that *Lixus praepotens* (Say) of Boheman (1836) is evidently this same species. *Lixus praepotens* (Say) of Boheman (1836) therefore represents only a reassignment from *Rhynchophorus* to *Lixus* and a species redescription, not description of a new species as indicated by Csiki (1934) and O'Brien and Wibmer (1982).

The holotype of *Cleonus inornatus* LeConte from Owen's Valley, California, as noted under "Notes about synonymy" section for *C. placidus*, although possessing a similar elytral scale pattern to *C. placidus* individuals, is here considered conspecific with *C. trivittatus*. This decision is based on the character states of the reduced extent of tarsal vestiture, presence of slight postocular lobes, and short dorsal erect vestiture on the pronotum shared with *C. trivittatus* and not *C. placidus*. *Cleonus (Cleonidius) bicarinatus* Casey is a typical, but abraded *C. trivittatus*.

Problems in recognition.— Specimens of *C. trivittatus* are most likely to be confused with those of *C. quadrilineatus*, *C. placidus* and *C. boucardi*. Discussions of characters allowing for separation of the former are given under the "Problems in recognition" section for each of the latter three species.

Description.— *Specimens examined.* 128 males, 159 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 31. *Size.* Length, male, 9.4–17.3 mm; female, 8.2–18.4 mm. Width, male, 3.8–9.4 mm; female, 3.0–8.2 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with punctures sparse to moderately dense, small, shallow, some large and longitudinally confluent immediately above eyes; interspersed with dense minute punctures. Frons also with sparse to moderately dense, elongate-narrow appressed to recumbent white scales medially, erect immediately above eyes. Frons separated from base of rostrum by shallow to moderately deep transverse impression (Fig. 153a). Base of median tumescence of rostrum with small, shallow fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.58-0.73 times length in male; 0.57-0.80 in female) (Fig. 153). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly to markedly medially tumescent from point of antennal insertion to middle of frons (especially basally) (Fig. 153a); not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to dense, small, shallow; dorsally interspersed with dense minute punctures. Dorsally either lacking suberect or erect vestiture or with at most sparse to moderately dense, short, suberect hair-like scales; also with moderately dense to dense, elongate-narrow, appressed to recumbent white scales laterally, scales sparser medially and apically. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate, slightly elevated broad glabrous line to slightly elevated narrow glabrous shiny line. Dorsal and lateral punctation small to moderately large, sparse to moderately dense, shallow to moderately deep; smaller and shallower apically; sparser and shallower on flanks; areas between larger dorsal punctures with dense

minute regularly impressed punctures. Lacking dorsal suberect or erect vestiture or with sparse to moderately dense, short, suberect hair-like scales each situated in large puncture (Fig. 153a). Scales dorsally absent to sparse small and fine along median line; moderately dense to dense, elongate-narrow, appressed in pair of narrow to broad apically slightly narrowed paramedian stripes; laterally, scales absent to sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-narrow. Median basal portion of disk shallowly to moderately deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes lacking (most specimens) to moderately developed (few specimens); postocular vibrissae of unequal length, moderately long to very long, greatest length (from one-half to slightly greater than two-thirds width of eye) behind base of eye (Fig. 153a). In dorsal view with lateral margins uniformly slightly arcuate to straight and convergent from base to apical one-quarter to one-third, slightly constricted at apical one-quarter to one-third, then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and lacking or with at most only very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion very short to short, approximately one-half length of posterior more angulate portion or less; posterior and anterior portions not to slightly differentiated by a shallow transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.55-0.62 times length in males; 0.52–0.61 in females) (Fig. 134). In dorsal view with lateral margins very slightly sinuate to moderately and evenly arcuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally lacking suberect or erect dorsal vestiture or with at most sparse, short suberect hair-like scales on declivity; sutural interval with dense, small, fine to elongate-fine white (rarely golden) scales; interval 2 with scales very sparse to dense small and fine; intervals 3 to 5 with scales dense large elongate-narrow; intervals 6 to 8 with scales absent to moderately dense small and fine to elongate-fine; intervals 9 to 11 with scales dense, large elongate-narrow; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales (Fig. 134). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small to large denticles in apical three-quarters; subapical tooth small to large, not to distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of male present as small elongate pads on apical one-third of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical three-quarters of article 3; of foretarsus and mesotarsus of female as apical tufts to small elongate-narrow pads on apical one-third of article 1, as rounded pads on apical one-quarter to one-half of article 2, and as large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male as elongate-narrow pad on apical one-quarter on inner lobe and as apical tuft on outer lobe of article 1, as elongate pads on apical one-half of article 2, as moderately large elongate-oval pads on apical one-half to three-quarters of article 3; of metatarsus of female as apical tuft to elongate-narrow pad on apical one-quarter on inner lobe and as elongate-narrow pad on apical one-half on outer lobe of article 1, as elongate pads on apical one-quarter to three-quarters of article 2, as elongate-oval pads on apical one-third to one-half of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow to moderately robust appressed white scales. Abdominal sterna III to VI (especially sterna III and IV) with distinct rounded glabrous patches, each with large puncture and single appressed to suberect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with very slightly developed median shiny tubercle. *Genitalia.* Female (six examined). Abdominal sternum VIII with basal arm short; lateral arms moderately inwardly arcuate throughout length; not to slightly expanded at apex (Fig. 173). Stylus moderately large compared to length of gonocoxite II. Male (six examined). Internal sac (Figs. 193a,b) elongate and low; median dorsal pocket low, with single moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired markedly dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with small paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket slightly emarginate medially in dorsal view (Fig. 193b). Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Individuals from the northern part of the species range (especially Alberta, Canada) possess moderately developed postocular lobes and correspondingly shorter postocular vibrissae. Throughout the rest of the species range, lobes are lacking or only slightly developed and postocular vibrissae are longer.

In the western part of the species range in California and Nevada (especially the former), individuals possess short suberect dorsal vestiture on the head and pronotum. Throughout the rest of the species range, dorsal suberect or erect dorsal vestiture is lacking or at most very short and indistinct.

Geographic distribution.— This species is widespread in the western United States of America and Canada from extreme southern British Columbia south to southern California in the west, and from southern Manitoba, south through eastern South Dakota, Kansas to western Texas (Fig. 220).

Natural history.— This species appears to be associated primarily with grassland and desert-grassland transitional habitats throughout the species range. Adults have been collected exclusively on Leguminosae as follows; *Astragalus* spp. (as "loco" or "locoweed"), *A. bisulcatus* (Hook.) Gray var. *haydenianus, A. earlei* Greene *ex.* Rydb., *A. flavus* Nutt., *A. utahensis* Torr. and Gray, *A. wootoni* Sheldon, *Oxytropis lambertii* Pursh, and *O. sericea* Nutt. Adults have been reared from *Astragalus* sp. (as "locoweed"). Adults have been collected throughout the year at elevations of from 131–3640 m (N=42) (Fig. 233).

A single specimen was found in the stomach contents of *Bufo* sp. (Amphibia).

Chorological relationships.— Table V.

Phylogenetic relationships.— Primary characters indicate only that this species is a member of an unresolved quadrichotomy composed of the four species in the *C. boucardi* group (Fig. 236). Distribution of the apotypic state of the secondary character of length of dorsal vestiture place this species as the sister-species to the *C. quadrilineatus-C. placidus* lineage in the *C. boucardi* group (Fig. 237).

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Cleonidius placidus Csiki
(Figs. 135, 154, 174, 194, 222)

</div>

Cleonus pacificus Fall 1901:260 [not Olivier 1807:268]. Holotype (examined), male, labelled "Redondo/ Cal.4.7.98", "TYPE/ *pacificus*", "M.C.Z./ Type/ 25194", "H.C.FALL/ COLLECTION", "*Cleonus/ pacificus/* Fall" (MCZC). Type locality, Redondo, California. Leng 1920 (catal.).
Cleonus (Cleonidius) placidus Csiki 1934:65. New name for *Cleonus pacificus* Fall. Blackwelder 1939 (check.).
Cleonis pacificus; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).
Cleonis placidus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— This species is commonly known as *C. pacificus* (Fall). This name is a junior homonym and *C. placidus* Csiki is the valid name. The holotype of *Cleonus inornatus* LeConte from Owen's Valley, California has an elytral scale pattern similar to that of *C. placidus* (Fig. 135) but differs in other structural features (possession of short dorsal suberect vestiture of the head and pronotum, slightly developed postocular lobes, and less extensive ventral tarsal pilosity) that are found in Californian *C. trivittatus. Cleonus inornatus* herein regarded as conspecific with *C. trivittatus* (see also "Notes about synonymy" section under *C. trivittatus*).

Problems in recognition.— Most individuals of this species are easily recognized by the lack of, or at most only very slightly developed postocular lobes (Fig. 154a), moderately long dorsal erect vestiture of the head and pronotum (Fig. 154a), and distinctive elytral scale pattern (Fig. 135). From *C. trivittatus*, most individuals are separated by the elytral scale pattern and also by the presence of moderately long dorsal erect vestiture on the head and pronotum in *C. placidus*; in *C. trivittatus*, dorsal erect or suberect vestiture is lacking or at most only suberect and short (Fig. 153a). The two species are also largely allopatric in their distributions; *C. placidus* is known only from California (Fig. 222), whereas *C. trivittatus* is widely distributed in western North America, but known from only a few localities in California (Fig. 220). These few *C. trivittatus* from California are difficult to separate from *C. placidus*, however, most of them possess short erect dorsal vestiture, whereas this vestiture is slightly longer on the head and pronotum of most *C. placidus*; they also possess less extensive ventral tarsal pilosity,

slightly developed postocular lobes, and lack the distinctive elytral scale pattern of *C. placidus*. Both species are known only from Leguminosae.

Cleonidius placidus individuals may also be confused with individuals of *C. quadrilineatus*, but as for *C. trivittatus* specimens, the distinctive scale pattern of *C. placidus* should serve to separate the two (Fig. 135). Otherwise, *C. placidus* is known only from Leguminosae and is found in California, whereas *C. quadrilineatus* is known from Rosaceae and Rhamnaceae (rarely from Leguminosae) and is widespread in southwestern North America (including California). Most individuals of *C. placidus* are also slightly larger than are most *C. quadrilineatus* (see Fig. 197).

Description.— *Specimens examined.* 57 males, 49 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 32. *Size.* Length, male, 9.9–17.1 mm; female, 12.6–17.6 mm. Width, male, 3.7–6.2 mm; female, 4.3–6.7 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with punctures sparse to moderately dense, small to moderately large, shallow, some longitudinally confluent immediately above eyes; interspersed with dense minute punctures. Frons also with moderately dense, moderately long, erect hair-like scales and sparse to dense, elongate-narrow appressed white scales medially, erect immediately above eyes. Frons continuous with base of rostrum or only slightly separated by shallow transverse impression (Fig. 154a). Base of median tumescence of rostrum with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.59-0.65 times length in male; 0.57-0.62 in female) (Fig. 154). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes visible. Rostrum slightly to moderately medially tumescent from point of antennal insertion to middle of frons (Fig. 154a); not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as rounded to sharp, narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to moderately dense, small to moderately large, shallow to moderately deep; punctures smaller and irregularly impressed apically, in some specimens dorsally interspersed with dense minute punctures. Dorsally with moderately dense, moderately long to long, erect hair-like scales; also with sparse, elongate-narrow, recumbent white scales laterally, scales sparser medially and apically. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate, slightly elevated broad glabrous line to slightly elevated narrow glabrous shiny line, well-developed and distinct in most specimens. Dorsal and lateral punctation moderately large, moderately dense to dense, moderately deep; smaller and shallower apically; sparser, smaller and shallower on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Dorsally, laterally and medially with moderately dense, moderately long to long, erect hair-like scales each situated in large puncture (Fig. 154a). Scales dorsally absent along broad median line; moderately dense to dense, elongate-narrow, appressed in pair of narrow apically convergent and slightly narrowed paramedian stripes; laterally, scales absent. Lateral margins and flanks with scales moderately dense to dense, elongate-narrow. Median basal portion of disk moderately deeply to deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes lacking (most specimens) to only very slightly developed (few specimens); postocular vibrissae of unequal length, very long, greatest length (slightly greater than two-thirds width of eye) behind base of eye (Fig. 154a). In dorsal view with lateral margins uniformly very slightly arcuate and convergent from base to apical one-quarter, slightly constricted at apical one-quarter, then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and lacking or with at most only very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion very short, indistinct. *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.51–0.56 times length in males; 0.50-0.57 in females) (Fig. 135). In dorsal view with lateral margins straight to very slightly sinuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally with sparse, short suberect hair-like scales (most evident on declivity); sutural interval with sparse to moderately dense, small fine white scales; interval 2 with irregularly distributed patches of dense, elongate-fine white scales, otherwise with scales absent to sparse, small and fine; intervals 3 to 11 with scales uniformly moderately dense to dense, elongate-fine to elongate-narrow (some specimens with irregularly distributed patches of even larger denser, white scales, especially on intervals 9 to 11) (Fig. 135). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of male present as elongate pads on apical two-thirds of article 1, as large rounded pads on apical two-thirds of article 2, and as large rounded pads on more or less entire ventral surface of article 3; of foretarsus of female as small elongate pads on apical one-third of article 1, as rounded pads on apical one-half of article 2, as large rounded pads on apical three-quarters of article 3; of mesotarsus of female as small elongate pads on apical one-quarter to one-third of article 1, as rounded pads on apical one-half of article 2, as large rounded pads on apical two-thirds of article 3; of metatarsus of male as elongate pads on apical one-half to two-thirds of article 1, as large rounded pads on apical two-thirds of article 2, as large rounded

pads on more or less entire ventral surface of article 3; of metatarsus of female as elongate-narrow pads on apical one-quarter to two-thirds of article 1, as elongate pads on apical one-half to two-thirds of article 2, as large rounded pads on apical two-thirds of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow to moderately robust appressed white scales; scales sparser along midline on sternum VII of female. Abdominal sterna III to VI (especially sterna III and IV) with distinct large rounded glabrous patches, each with large puncture and single recumbent to suberect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with very slightly developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm moderate in length; lateral arms moderately inwardly arcuate at midlength; slightly expanded at apex (Fig. 174). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 194a,b) elongate and low; median dorsal pocket low, with single moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with moderately large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket bisinuate medially in dorsal view (Fig. 194b). Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from California in the coastal and central valleys from San Francisco south to San Diego (Fig. 222).

Natural history.— This species is found only in the Pacific semi-desert region. Adults have been collected almost exclusively from *Astragalus* spp. (Leguminosae). A single specimen was collected on parsnip, *Pastinaca sativa* L. (Umbelliferae). Adults have also been reared from roots of *Astragalus* sp. Adults have been collected throughout the year at elevations of from 9–1747 m (N = 10) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. quadrilineatus*, the two species forming a lineage that is the sister group of *C. trivittatus* (Fig. 237).

Cleonidius quadrilineatus (Chevrolat)
(Figs. 136, 155, 175, 195, 224)

Apleurus quadrilineatus Chevrolat 1873:80. Holotype (examined), male, labelled "66", "ex coll./ Sallè", "MUSÉUM PARIS/ 1952/ COLL R OBERTHUR", "*apleurus/ quadrilineatus/* Chev. type texas", and with an inverted label "*Lixus/ praepotens/* Boh. Texas", and with a label indicating it as the holotype "*Apleurus/ quadrilineatus/* Chev. HOLOTYPE/ labelled Anderson" (MNHP). Type locality, Texas.
Cleonus quadrilineatus; LeConte 1876a (key, diag.). Henshaw 1885 (check.). Wickham 1889. Wickham 1896 (check.). Fall 1897. Fall 1901. Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Pierce 1907 (biol., misident. of *Cleonidius trivittatus*). Chittenden 1911 (biol., misident. of *Cleonidius trivittatus*). Anderson 1914 (misident. of *Cleonidius poricollis*). Blatchley and Leng 1916 (figure, misident. of *Cleonidius trivittatus*). Yothers 1916 (prob. misident. of *Cleonidius trivittatus*, in part). Leng 1920 (catal.). Essig 1958 (biol., misident. of *Cleonidius trivittatus*). Arnett *et al.* 1980 (key, redesc., biol., misident. of *Cleonidius trivittatus*).
Lixus texanus; LeConte 1876a (in part, mixed type series).
Cleonus (Cleonidius) quadrilineatus; Casey 1891 (key). Csiki 1934 (catal.). Hatch 1971 (key, redesc., misident. of *Cleonidius poricollis*).
Cleonis quadrilineatus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— The holotype of *C. quadrilineatus* is the typical elongate-narrow Rosaceae form. Many published references to *C. trivittatus* are to this species.

Problems in recognition.— Specimens of *C. quadrilineatus* are very likely to be commonly confused with those of the broadly sympatric *C. trivittatus. Cleonidius quadrilineatus* specimens are separated from the latter by their more elongate-narrow elytral form (Fig. 136) and by presence of moderately long erect hair-like scales on the pronotal disk (Fig. 155a), which in *C. trivittatus* are at most only short, suberect and indistinct (Fig. 153a). Most *C. quadrilineatus* are also associated with Rosaceae or Rhamnaceae, although rarely also with

Leguminosae, whereas all *C. trivittatus* are associated with Leguminosae. Some *C. trivittatus* have slightly to moderately developed postocular lobes (especially from the northern part of the range) whereas all *C. quadrilineatus* lack postocular lobes entirely (Fig. 155a).

In California, specimens of *C. quadrilineatus* may be confused with *C. placidus*, especially specimens of the latter in which the distinctive elytral scale pattern (Fig. 135) is abraded. Individuals of *C. placidus* have moderately long, erect hair-like scales on the pronotum (Fig. 154a), as do *C. quadrilineatus*, but are associated exclusively with Leguminosae. *C. placidus* individuals are also slightly larger than are those of *C. quadrilineatus* (Fig. 197) and have slightly more extensive ventral tarsal pilosity.

Description.— *Specimens examined.* 108 males, 107 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEl, and LP/LEl are presented in Table 33. *Size.* Length, male, 8.3–14.3 mm; female, 9.3–13.1 mm. Width, male, 2.9–5.3 mm; female, 3.2–4.8 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with punctures sparse to moderately dense, small to moderately large, shallow, some large and longitudinally confluent immediately above eyes; interspersed with minute punctures. Frons also with sparse to moderately dense, elongate-narrow appressed white scales medially, erect immediately above eyes. Frons continuous with base of rostrum or separated from base of rostrum by shallow transverse impression (Fig. 155a). Base of median tumescence of rostrum with small, shallow fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.60-0.70 times length in male; 0.58-0.69 in female) (Fig. 155). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum moderately medially tumescent from point of antennal insertion to middle of frons (especially basally) (Fig. 155a); not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to dense, small to moderately large, shallow; punctures smaller apically; dorsally interspersed with dense minute punctures. Dorsally with moderately dense, moderately long, suberect to erect, hair-like scales (especially laterally); also with moderately dense, elongate-narrow, recumbent white scales laterally, scales absent to sparse medially and apically. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate, slightly elevated broad glabrous line to slightly elevated narrow glabrous shiny distinct line. Dorsal and lateral punctation moderately large, moderately dense, moderately deep; smaller and shallower apically; sparser and shallower on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Dorsally, laterally and medially, with moderately dense, moderately long, erect hair-like scales each situated in large puncture (Fig. 155a). Scales dorsally absent to sparse small and fine along median line; moderately dense, elongate-fine to elongate-narrow, appressed in pair of narrow apically slightly narrowed paramedian stripes; laterally, scales absent to sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed in moderately broad stripe. Flanks with scales moderately dense, elongate-fine to elongate-narrow. Median basal portion of disk shallowly to moderately deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes lacking; postocular vibrissae of unequal length, very long, greatest length (greater than two-thirds width of eye) behind base of eye (Fig. 155a). In dorsal view with lateral margins uniformly slightly arcuate and convergent from base to apex, to straight and convergent from base to apical one-quarter to one-third, slightly constricted at apical one-quarter to one-third, then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion very short, indistinct. *Elytra.* Elongate-narrow in general form (width at midlength 0.48-0.55 times length in males; 0.48-0.52 in females) (Fig. 136). In dorsal view with lateral margins straight to very slightly sinuate slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally with sparse, short suberect hair-like scales (most evident on declivity); sutural interval with dense, small fine golden to white scales; interval 2 with scales very sparse to dense small and fine, white; intervals 3 to 5 with scales dense large elongate-narrow, white; intervals 6 to 8 with scales sparse to moderately dense, small and fine to elongate-fine, white; intervals 9 to 11 with scales dense, large elongate-narrow, white; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales (Fig. 136). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small to moderately large denticles in apical three-quarters; subapical tooth indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of male present as small elongate pads on apical one-half of article 1, as large, elongate-oval pads on apical two-thirds of article 2, and as large rounded pads on apical three-quarters of article 3; of foretarsus and mesotarsus of female as as small elongate-narrow pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, and as moderately large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male as elongate-narrow pad on apical one-half on inner lobe and apical one-third on outer lobe of article 1, as elongate pads on apical one-half to two-thirds of article 2, as large rounded pads on apical three-quarters of article 3; of metatarsus of female as

elongate-very-narrow pad on apical one-half on inner lobe and apical one-third on outer lobe of article 1, as elongate pads on apical one-third to one-half of article 2, as moderately large elongate-oval pads on apical one-half to two-thirds of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow to moderately robust appressed white scales. Abdominal sterna III to VI (especially sterna III and IV) with distinct rounded glabrous patches, each with large puncture and single appressed to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to moderately developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms moderately inwardly arcuate throughout length; not to slightly expanded at apex (Fig. 175). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 195a,b) elongate and low; median dorsal pocket low, with single moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired markedly dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with small paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket slightly emarginate medially in dorsal view (Fig. 195b). Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is found from California east to eastern Nebraska, Oklahoma, and central Texas (Fig. 224). There is a single Mexican record from near Zacatecas.

Natural history.— This species is found primarily in the western xerophytic evergreen forest region but also in desert-grassland transitional habitats. Many adults have been collected primarily on Rosaceae or Rhamnaceae, especially in oak-pinyon-juniper woodlands throughout the species range; a few have been found on Leguminosae in Arizona. Adults have been collected on *Astragalus wootoni* Sheldon, *Lupinus* sp. (Leguminosae); *Ceanothus* sp. (Rhamnaceae); *Cercocarpus montanus* Raf., *Rosa* sp. (Rosaceae). Adults have been reared only from *Astragalus* sp. roots at Sulphur Springs Valley, Arizona. I suspect that a variety of Rosaceae or Rhamnaceae serve as hosts at higher altitudes throughout the species range. Adults have been collected from January to October at elevations from 15–4186 m (N=63) (Fig. 233).

Adults have been found in the stomach contents of *Geococcyx californicus'* (roadrunner; Aves) at Carlsbad, New Mexico.

Other individuals and I have collected this species and *C. texanus* together on various Rosaceae and Rhamnaceae in Texas and Arizona.

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. placidus*, the two species forming a lineage that is the sister group of *C. trivittatus* (Fig. 237).

Incertae sedis

This category is used herein for a single species of uncertain placement, *Cleonidius vibex* (Pallas). Although adults of *C. vibex* have a vittate elytral scale pattern, lack extensive ventral tarsal pilose pads, possess a moderately broad rostrum, and are brachypterous, all of which suggest inclusion in the *C. americanus* group, the nature of formation of the vittate scale pattern is fundamentally different from that in other *Cleonidius* and thus not homologous. In other *Cleonidius* the vittate pattern is produced as a result of differing sizes and densities of scales on the various elytral intervals; in *C. vibex*, the pattern is apparently produced as a result of presence or absence of white pigment in the individual scales. This suggests independent derivation of a vittate elytal pattern and perhaps of states of other characters as well.

Placement of *C. vibex* as sister to the remainder of *Cleonidius* can only be substantiated by an adaptive argument concerning the low likelihood of evolution of the fundamentally different vittate elytral scale pattern of that species from the scale pattern of other *Cleonidius*, which is formed in a very different non-homologous manner.

<div align="center">

Cleonidius vibex (Pallas), new combination

(Figs. 156, 176, 196)

</div>

Curculio vibex Pallas 1781:32. Types not examined. Herbst 1795.
Lixus denudatus Zoubkoff 1833:319. Types not examined. Faust 1890. Petri 1912.
Lixus karelini Boheman 1836:22. Types not examined. Faust 1890. Petri 1912.
Lixus vibex; Boheman 1836. Capiomont and Leprieur 1874. Faust 1890. Petri 1912. Lukjanovitsh 1926.
Lixus vibex scutellaris Petri 1905:103. Types not examined.
Lixus (Lixestus) vibex; Reitter 1916. Csiki 1934.
Lixus (Lixesthus) vibex; Ter-Minasyan 1978.

Notes about synonymy.— No types associated with the names recorded above have been examined by me. Synonymy presented here follows Petri (1912) and Csiki (1934).

Two additional species have been placed in *Lixus (Lixestus)* by Ter-Minasyan (1978). These are *L. pallasi* Faust and *L. meles* Boheman. These species will likely also prove to be *Cleonidius* but representatives have not been examined by me.

Problems in recognition.— Individuals of this species are easily distinguished from Nearctic *Cleonidius* by the widely divergent tarsal claws each lacking a basal internal flange, and the large unci especially on the fore- and mesotibiae. The rostrum of this species has uniformly very dense and small punctures, but no or else very few larger punctures typical of Nearctic species of *Cleonidius*. Individuals also differ from those of Nearctic species in that the contrasting dark and light areas of the pronotum and elytra are a result of apparently having white scales, such that the underlying dark cuticle is obscured, or unpigmented, such that the dark cuticle is not obscured. Individuals of Nearctic species on the other hand, have a vittate elytral scale pattern and a pronotal scale pattern that is a result of differing sizes of scales; small scales do not obscure the dark cuticle, whereas larger scales do.

The robust, downwardly curved rostrum and elytral scale pattern of individuals of this species result in superficial resemblance to *C. canescens*.

Description.— *Specimens examined.* 1 male, 1 female. *Size.* Length, male, 7.3 mm; female, 7.1 mm. Width, male, 2.7 mm; female, 2.6 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with only uniformly very dense minute punctures. Frons also with very dense, truncate grey-brown appressed scales. Frons continuous with base of rostrum (Fig. 156a). Base of median tumescence or carina of rostrum (if present) with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.73 times length in male; 0.75 in female) (Fig. 156). In lateral view moderately curved downward. In dorsal view with postgenae very slightly laterally expanded, antennal scrobes distinctly visible. Rostrum markedly medially tumescent from point of antennal insertion to middle of frons (Fig. 156a); not laterally expanded at midlength; lateral margins more or less rounded, not sharp; with median carina absent. Dorsal and lateral punctation very sparse, small, shallow; sparser apically and medially; dorsally interspersed with minute punctures. Dorsally lacking suberect or erect vestiture, with only uniformly very dense, appressed truncate grey-brown scales (punctation almost completely obscured), sparser apically and medially. Epistoma not swollen. *Pronotum.* Median carina lacking. Dorsal and lateral punctation sparse, small, shallow, interspersed with very dense minute regularly impressed punctures. Suberect or erect vestiture lacking. Scales dorsally uniformly dense small truncate appressed medially; laterally transparent in pair of narrow stripes (apparently black). Lateral margins and flanks with scales uniformly dense, small, truncate and appressed, punctation almost completely obscured. Median basal area of disk broadly and very shallowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae short, of uniform length (Fig. 156a). In dorsal view with lateral margins straight and convergent from apical one-third to base; slightly arcuate from apical one-third to apex; subapical constriction indistinct. *Prosternum.* With moderately large, moderately deep impression anterior to each procoxal cavity; swelling lacking. In lateral view with anterior flat to slightly angulate portion moderately long, approximately one-half length of posterior more angulate portion; anterior and posterior portions slightly differentiated by shallow transverse impression. *Elytra.* Moderately

elongate-narrow in general form (width at midlength 0.52 times length in male; 0.53 in female). In dorsal view with lateral margins very slightly sinuate and slightly convergent from apical one-third to humerus; moderately arcuate at apical one-third then straight and convergent to apex. Elytral apices not produced, rounded, slightly divergent. Humerus rounded, indistinct. Dorsally lacking suberect or erect vestiture. Scales uniformly very dense, small, robust, appressed grey-brown on sutural interval and intervals 2 to 5 and 8 to 11; intervals 6 and 7 with scales truncate, transparent, underlying dark cuticle visible through scales. Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings.* Moderate (slightly shorter than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; no distinct subapical tooth present. Foretibial and mesotibial unci of both sexes very large, metatibial uncus moderately large. Tarsal claws widely divergent, each lacking distinct basal internal flange. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of both sexes lacking from articles 1 and 2, present as small rounded apical tuft of article 3; of metatarsus of both sexes, lacking from articles 1 and 2, present as minute apical tuft of article 3. *Abdomen.* Ventral surface with dense, truncate, small appressed grey-brown scales. Abdominal sterna III to VI sparse moderately large shallow punctures, no distinct glabrous patches or suberect or erect vestiture present. Base of abdominal sternum VII of female internally (dorsally) with at most moderately-developed median shiny tubercle. *Genitalia.* Female (one examined). Abdominal sternum VIII with basal arm long; lateral arms straight and divergent from base to approximately apical one-third; moderately inwardly arcuate at apical one-third and slightly convergent to apex; apices moderately expanded (Fig. 176). Stylus moderately large compared to length of gonocoxite II. Male (one examined). Internal sac (Figs. 196a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third at dorsal margin (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket individually distinct from median dorsal pocket; apex of median dorsal pocket rounded in dorsal view. Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— Southern Russia, Persia, Siberia and Mongolia (Csiki 1934).

Natural history.— No information is available about the natural history of this species. Based on its general geographic distribution I suspect that it is a grassland or semi-desert inhabiting species.

Chorological relationships.— This is the only Palearctic species of *Cleonidius* I have seen.

Phylogenetic relationships.— See *"Incertae sedis"* section preceding.

Nomen dubium

Lixus californicus Motschulsky is herein treated as a *nomen dubium*. Motschulsky (1845:378) in his original description of this species noted only that its type was smaller, more elongate, and whiter than specimens of either *Lixus poricollis* Mannerheim and *L. modestus* Mannerheim. He further stated that he thought it likely that it was a male of *L. modestus*. Based upon examination of the holotype (on loan from Zoological Museum of the Moscow Lomonosov State University) *Lixus modestus* Mannerheim is, however, not a *Cleonidius* nor is it conspecific with any North American *Lixus* species known to me. Furthermore, *L. modestus* does not possess character states of the New World *Lixus* species component and thus I suspect has been erroneously labelled as having been collected in California. This notion of a misidentified type locality is supported by Mannerheim (1843: 291), who stated that Eschscholtz (*in litteris*) had referred to *L. modestus* or *Lixus adspersus* (a species described by Boheman (1836) from the Republic of South Africa).

In view of this confusion regarding the type locality of *Lixus modestus* Mannerheim, the statement by Motschulsky (1845) that he suspects *L. californicus* Motschulsky is a male of *L. modestus* (the type of *L. modestus* incidentally is a male), and the inadequate characterization (and the apparent loss of type material) of *L. californicus*, I consider recognition of *Lixus californicus* Motschulsky as a *nomen dubium* to be in the best interests of a stable nomenclature.

ADVENTITIOUS TAXA

During the course of study, individuals of two adventitious species were encountered from North American localities. These are *Stephanocleonus glaucus* labelled "S.C." (1), and "Ames, Iowa" (1); and, an unidentified species of *Tetragonothorax* from "Mobile, Alabama" (1). These species are considered not to be established in North America.

EXTANT TAXA ERRONEOUSLY PLACED IN CLEONINAE

Cleonis chilensis Blanchard 1851:326 is listed in both *Cleonus (Incertae Sedis)* and *Adioristus* in the Coleopterorum Catalogus (Csiki 1934; Schenkling and Marshall 1931) and also in Blackwelder (1947). Kuschel (1949:31) subsequently placed it in *Scotoeborus* (Leptopiinae [now Entiminae], Cylydrorhinini). I have examined the type of this species (deposited in MHNP) and agree that it is not cleonine.

Argentinorhynchus breyeri Brèthes 1910:211 was described from Argentina and originally noted as "Cleonidarum". It has since been regarded as cleonine by (Csiki 1934) who placed the genus as a subgenus of *Cleonus*. Likewise, and probably following Csiki, Blackwelder (1947) lists the species in *Cleonus*. Kuschel (1950:112) subsequently returned *Argentinorhynchus* to generic status and placed it in Erirhininae. The holotype of this species is located in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" but has not been examined by me (Bachman *in litt.*, 1985).

The genus *Lepyrus* is also not Cleoninae and has been removed to Molytinae (Hylobiinae of authors) (Solari 1941; Ter-Minasyan 1963).

FOSSIL MATERIAL

Various Tertiary coleopterous fossils have been identified as Cleoninae but, preservation is such that most of these are actually not reliably identifiable to subfamily, according to Kingsolver (1961) who has examined much of the material of Scudder (1893) and Wickham (1911, 1912) deposited at the Museum of Comparative Zoology, Harvard University. Matthews (1977) also notes a *Cleonus* sp. from the Tertiary of Banks Island in the Canadian Arctic but this identification is based only on elytral fragments. I have not examined any of these specimens.

Sleeper (1969) described two species of *Cleonidius* (as *Cleonus*) from Pleistocene Rita Blanca Lake deposits in Texas. Unfortunately I have not seen the specimens, and descriptions and figures do not provide information permitting meaningful comparison with extant species. Sleeper (1969) states that *Cleonidius ritablancensis* is near *Cleonidius sparsus* and that *Cleonidius channingensis* is near *Cleonidius circumductus*, but, the history of misidentification in *Cleonidius* and subtle differences between many of the species necessitates re-examination. Unfortunately location of the specimen depository was not stated by Sleeper (1969).

Fossils of species identified as the genus *Cleonus* are frequently encountered in late Pleistocene deposits in northern North America (Matthews, 1974, 1975; Hughes *et al.*, 1981; Mott *et al.*, 1981; Morlan and Matthews, 1983). Some of these have been tentatively identified as *Cleonus plumbeus*, but as noted by Morgan *et al.* (1985), they may actually represent one or more Palearctic species or even one of the herein-newly-described Nearctic species. All of this northern Pleistocene material actually belongs in the genus *Stephanocleonus*, and the present

revision of North American members of that genus reveals that taxa traditionally regarded as *S. plumbeus* are a complex of six species, four of which are newly described herein. All of this fossil material is deposited with John V. Matthews, Jr., Geological Survey of Canada, Ottawa; none of it has been examined by me.

EVOLUTIONARY ANALYSIS: RECONSTRUCTED PHYLOGENY

My profession embodies one theme even more inclusive than evolution--the nature and meaning of history. History employs evolution to structure biological events in time. History subverts the stereotype of science as a precise, heartless enterprise that strips the uniqueness from any complexity and reduces everything to timeless, repeatable, controlled experiments in a laboratory. Historical sciences are different, not lesser. Their methods are comparative, not always experimental; they explain, but usually do not try to predict; they recognize the irreducible quirkiness that history entails, and acknowledge the limited power of present circumstances to impose or elicit optimal solutions.

Steven Jay Gould, Prologue to "The Flamingo's Smile", 1985.

Inquiry in historical science proceeds primarily by investigation of relationships between pattern and process. Factual data are assembled and patterns are searched for and recognized in these data. Recognition of a pattern, especially if repeated within the study group or in other groups, begs explanation by proposal of a common causal mechanism in the form of a testable hypothesis. Proposal and subsequent testing of this hypothesis, the former inductive, the latter hypothetico-deductive, are the cornerstones of science in general and systematic research in particular. Comparison of these approaches in systematics is adequately treated by Wiley (1981) and application of the hypothetico-deductive method to systematics by Gaffney (1979).

In this study, aspects of both inductive and hypothetico-deductive science are employed and applied. Although some recent authors advocate only the hypothetico-deductive approach, I believe that much useful information and advances in biological knowledge have been and should continue to be, achieved through use of both approaches, but that they operate best at different stages in the process of scientific inquiry; induction for hypothesis formulation, deduction for hypothesis testing.

Herein, an inductive approach is used primarily to attempt to formulate explanations of details of the evolutionary and biogeographic history of the weevil subfamily Cleoninae, especially species of the genera *Cleonidius* and *Apleurus* in North America. From these analyses, evident patterns are identified and more general hypotheses concerning biogeographic patterns and evolutionary trends in arid-land-adapted organisms are proposed, to be available for subsequent testing in future studies for their applicability and predictive value. In addition, some competing and previously proposed hypotheses concerning general evolutionary or biogeographic patterns are tested by application of the appropriate results of this study of North American Cleoninae.

Methods of phylogeny reconstruction

Since the publication of Hennig (1966), there has been an expanding emphasis on both theoretical and practical aspects of phylogenetic and biogeographic studies. While the pages of *Systematic Zoology* clearly document an intense interest in theoretical aspects, increased attention to practical aspects and applications is evidenced simply by the numbers of revisionary works that deal extensively with reconstruction of phylogeny and its applicability to character evolution, classification and biogeography. The appeal of the phylogenetic approach (Hennig, 1966) to phylogeny reconstruction over various other approaches (Wiley, 1981) is

primarily in the potential for critical assessment of resultant hypotheses of relationship, their logical predictive nature and their general applicability. The approach I have taken herein is phylogenetic (Hennig, 1966). Character states are determined as apotypic (derived) or plesiotypic (primitive) and only distributions of apotypic states are used in the analysis.

Of paramount importance in reconstructing phylogeny are: one, determination of polarity of character states; and two, recognition of homoplasy or simply, determination of which characters actually reflect descent from a common ancestor, not other processes.

Out-group criteria were used to polarize character states of all primary characters (Watrous and Wheeler, 1981). For secondary characters, out-group criteria were employed where possible although in-group or local parsimony (Maddison *et al.*, 1984), or the functional out-group of Watrous and Wheeler (1981), were also used, especially in instances where more than one character state occurs in the out-groups or where, although both out-groups have the same state, there is incompatibility with the reconstructed phylogeny as determined by primary characters.

Character weighting was employed. Characters used in the phylogenetic analysis of species in *Cleonidius* and *Apleurus* are considered at two levels as indicated above. Primary characters are those which are deemed of high weight because there is no ambiguity in determining polarity of the various character states based on an out-group analysis (Watrous and Wheeler, 1981; Maddison *et al.*, 1984), and the apotypic state, so determined, is not widely distributed elsewhere in Cleoninae. Characters meeting these criteria are given further support as primary characters should they, as a group, result in a reconstructed phylogeny of the genus in question in which the distributions of apotypic states of the various characters are compatible, with the result that there is minimal homoplasy. Characters that exhibit more than a little homoplasy elsewhere in Cleoninae may be regarded as primary should the distribution of their apotypic states be entirely compatible with the distribution of apotypic states of numerous other primary characters.

Secondary characters are those considered to be of lesser weight because of widespread presence of the apotypic state elsewhere in Cleoninae. Lack of complete compatibility with primary characters, and/or problems in determining polarity of the character states based strictly on an out-group analysis necessitating reference to in-group relationships previously resolved on the basis of the distribution of states of primary characters also results in such characters being considered at a secondary level. Distribution of apotypic states of secondary characters may or may not be compatible with distributions of apotypic states of primary or other secondary characters with the result that there is generally more homoplasy in characters included in this more resolved reconstructed phylogeny of the genus is question.

Characters examined but not included in the phylogenetic analysis are those that exhibit extensive homoplasy elsewhere in Cleoninae and are not compatible with, or, when compared with other potential secondary characters, exhibit minimal compatibility with, distributions of apotypic states of primary characters.

Primary characters are the characters used to establish a basic set of relationships that may or may not be totally dichotomously resolved, but in which confidence can generally be regarded as high. This set of relationships is then accepted *a priori* and the distribution of states of secondary characters considered with reference to this reconstructed phylogeny. Thus secondary characters can only be used to reinforce previously established relationships or to further resolve the reconstructed phylogeny by providing additional characters in which confidence is low.

I do not use a complex system of weighting characters such as that of Hecht and Edwards (1976, 1977). Instead, I use this simple two level weighting system which depends solely upon the distributions of character states, and makes no inferences or assumptions about complexity, function or adaptive value which may not have a logically sound basis. As such, I think this system better reflects the confidence level for a given set of relationships especially when these are depicted on successively more resolved cladograms.

Phylogenetic position of Cleoninae

The detailed phylogenetic position of Cleoninae is unclear although relationships at some level appear to be with Molytinae, specifically the Hylobiinae, of authors. Taxonomy of these two subfamilies has a history of repeated misclassification and a repeated concern for adequate distinction (Aslam, 1963; Marshall, 1932; Solari, 1941; Ter-Minasyan, 1963). In addition, Aslam (1961) has noted that among Curculionidae, the Molytinae and Cleoninae are unique in their possession of free-lobed testes, and, along with a few other subfamilies, both have the vasa efferentia free from the testicular lobes and each of the latter with numerous follicles. These states however, all appear to be symplesiotypic for they are all found in primitive Curculionoidea (Morimoto, 1962) and cannot be considered evidence for a sister-group relationship but rather, as will be noted forthwith, for a primitive position for Cleoninae with respect to other Curculionidae. Although unjustified by synapotypy as sister-taxon to Cleoninae, certain Molytinae are employed herein as the out-group for the purpose of tentative polarization of character states in genera of Cleoninae.

Evidence that Cleoninae are a very primitive lineage within Curculionidae is extensive. Indeed they may prove sister to the rest of the Curculionidae based on the large number of plesiotypic character states that they possess.

Buchner (1933, 1953) and Scheinert (1933) discuss at length the mechanism by which adult female Cleoninae pass on symbiotic bacteria to the egg and site of localization of these symbionts in the larvae. In Cleoninae, symbiont pouches are paired and attach to the vagina near the base of gonocoxite II. Bacteria develop in these pouches embedded in a secretion originating from the epithelial cells of the pouch. As eggs pass through the vagina they are coated with bacteria which are then ingested by young larvae. In the larvae, there are four variously shaped evaginations in the anterior part of the midgut where the bacteria are localized. Both of these states are unique within Curculionidae to Cleoninae and are very similar to those of Anobiidae, Lagriidae and Cerambycidae (Buchner, 1953). Recently, Mann and Crowson (1984) noted that similar pouches to those in adult female Cleoninae also occur in various Chrysomelidae, a constituent taxon of the presumed sister-lineage of Curculionoidea; site of localization in larvae was not examined. Although Curculionoidea generally regarded to be primitive have not been examined for these characters, the widespread distribution of the states in related groups suggests that these states are plesiotypic in Curculionidae and that Cleoninae is a very primitive lineage within that family.

Wing structure is also primitive (Kingsolver, 1961), because in at least some Cleoninae, the branches of the second anal vein are joined at the base and the basal one-half of the first anal vein is present. These features appear to be unique to Cleoninae within Curculionidae and are undoubtedly plesiotypic because they are found in primitive Curculionoidea.

Ting (1936) has also noted that in Curculionidae, Cleoninae are the only subfamily in which adults have the labial palpi ventral in their site of attachment to the labium. Although Ting (1936) suggests this to be the autapotypic state, the fact that the same state is found in

primitive Curculionoidea suggests that it is plesiotypic.

Further evidence for a primitive phylogenetic position for the subfamily comes from the structure of the testes (as noted previously), and generalized stem or root mining habits of larvae of the subfamily.

Monophyly of Cleoninae is indicated by structure of the labial palpi, which, although described as of one article (Aslam, 1963; Ter-Minasyan, 1963), are of three very small and telescoped articles (Figs. 61–63). This character state appears to be unique to Cleoninae within Curculionoidea. Most other Curculionoidea possess larger three-segmented labial palpi; some lack palpi entirely or have the palpi variously modified, but these latter states are clearly autapotypic. At present, this is the only autapotypic character state supporting monophyly of Cleoninae.

Phylogenetic relationships among tribes of Cleoninae

Within Cleoninae, Csiki (1934) recognized four tribes: Lepyrini, Cleonini, Rhinocyllini, and Lixini. Lepyrini, has since been removed from Cleoninae and placed in Molytinae (Solari, 1941; Ter-Minasyan, 1963). Since then, Aslam (1963) and Ter-Minasyan (1978) have recognized only two tribes, Cleonini and Lixini; O'Brien and Wibmer (1982) continue to recognize three tribes, as above, excluding Lepyrini.

In general, the tribe Lixini are all those Cleoninae whose adults have a more elongate-narrow cylindrical rostrum and elongate-narrow body form. The tribe Cleonini on the other hand, includes taxa whose adults have a more robust rostrum and body form. Cleonini are generally associated with arid habitats; Lixini, with mesic habitats. Rhinocyllini, when used, is reserved for the genera *Rhinocyllus* and *Bangasternus* which are otherwise placed as Lixini.

No satisfactory suprageneric classification has been proposed for Cleoninae, because the phylogenetic relationships of the world genera must be assessed before such can be realized. No tribal placement is therefore herein attempted although generic relationships of North American taxa, traditionally placed as Cleonini, are discussed and represent a start at a reconstructed phylogeny of genera and revised tribal classification.

Phylogenetic relationships of genera of New World Cleonini

In an attempt to determine the relative position of *Apleurus* and *Cleonidius*, a survey of representatives of 50 genera of world Cleoninae was undertaken (Appendix 2). In instances where type species have not been designated for a given genus, the species considered representative of that genus is one originally included and which could subsequently be designated as the type species. Where possible, relationships were inferred on the basis of shared, presumably derived character states, preferably unique to those taxa or found in few other Cleoninae (preferably those taxa, which for reasons of distribution of other more widespread and presumably apotypic character states, are not considered closely related to the genus under study). Inferred monophyly of this grouping was then corroborated by examination of distribution of either apotypic or plesiotypic states of other characters (with more widespread distributions) for concordance.

Confidence in phylogenetic relationships of *Apleurus* is high because a large number of representatives of genus-group names in Cleonini were examined and considered in the search for out-groups. Unfortunately, confidence in out-group relationships of *Cleonidius* is low, largely because few representatives of genus-group names of Lixini were examined. Although *Cleonidius* has traditionally been considered a member of Cleonini (the initial seach for an

out-group accepted that premise), indications are that *Cleonidius* (and *Cylindropterus*) is more closely related to Lixini than to any traditional Cleonini. In fact, as noted elsewhere, some *Lixus* species proved to belong in *Cleonidius*. A revision of this large and structurally divergent genus is required on a world basis to better formulate the phylogenetic relationships of *Cleonidius*.

For *Apleurus*, out-groups *Cnemodontus* and *Chromoderus*, together with *Apleurus* itself, are inferred to compose a monophyletic group based primarily upon presence of a variously developed acute pronotal postocular projection fringed with anteriorly directed, long, postocular vibrissae of unequal length (Figs. 81–88). This state is otherwise found only in species of *Lixus* (Fig. 4), *Lixocleonus* and *Microlarinus* (Fig. 1), taxa that on the basis of distributions of states of other characters are not considered closely related to *Apleurus*.

Recognition of this group as monophyletic is supported by the distributions of the following character states, which are shared, except as noted, by members of the three genera and in most instances, by a variable number of other genera as well. Polarity of the states of these characters may or may not have been determined.

1. Body form more or less robust. The three taxa under consideration possess this state as do numerous other Cleoninae. Molytinae of phylogenetic interest are also more or less robust in body form; therefore, this state is likely plesiotypic.

2. Pronotum with scale pattern with large white scales present in a lateral stripe of variable width, small and fine in a moderately broad to very broad apically narrowed median stripe; median area largely black in color, the underlying dark cuticle not obscured by the overlying scales (Figs. 24, 68–80). This state is present in *Apleurus* and *Chromoderus*, as well as numerous other genera of Cleoninae. A distinct pronotal scale pattern is not evident in *Cnemodontus*. Polarity of the states of this character has not been determined.

3. Eye like an inverted, elongate teardrop in shape. This state is found in the three genera in question as well as in numerous other genera of Cleoninae. Polarity of the states of this character has not been determined.

4. Eye prominent and convex in dorsal view. This state is found in *Apleurus* and *Cnemodontus* (but not *Chromoderus*), as well as in various *Lixus* species and *Lixocleonus*. Polarity of the states of this character has not been determined.

5. Female with abdominal sternum VIII with basal arm absent (Figs. 56e-57e, 89a-96a). This state is found in all three genera as well as in numerous other genera of Cleoninae. Molytinae possess a long basal arm and thus lack of the arm is likely apotypic but also homoplasious.

6. Tarsi with articles moderately wide, not markedly elongate-narrow. This state is found in *Chromoderus*, *Cnemodontus* and some *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

7. Tarsi with ventral pilose pads present, large and distinctly delimited. This state is found in *Chromoderus*, *Cnemodontus* and some *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

8. Pronotum with dorsal surface punctate, not tuberculate. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

9. Female with spermathecal gland spherical, not variously elongate and cylindrical. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

10. Rostrum moderately elongate-narrow to robust. This state is found in the three taxa in question as well as various other Cleoninae. Polarity of the states of this character has not been determined.

11. Tibiae with corbel ridge sharp (as in Fig. 6). This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

12. Ventral surface of male lacking extensive long erect vestiture. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

13. Female with gonocoxite II triangular in shape (Figs. 89b–96b), apex not prolonged into a marked lobe (Fig. 54). This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

14. Antenna with apical three articles with placoidal sensilla. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as various other Cleoninae. Polarity of the states of this character has not been determined and not all Cleoninae have been examined in detail for this character.

For *Cleonidius*, out-groups *Lixus (Lixoglyptus)* and *Cylindropterus* were selected largely because of their close resemblance to *Cleonidius* species, yet lack of the internal swelling at the base of abdominal sternum VII in the female which characterizes the latter. No synapotypies were identified to unite the three taxa as a monophyletic group and indeed, the group may prove to be paraphyletic. Distributions of the states of the following characters support a close but unresolved relationship among these three taxa.

1. Body form more or less elongate-narrow, cylindrical. The three taxa under consideration possess this state as do *Mecaspis*, *Lixocleonus*, and most *Lixus*. Molytinae of phylogenetic interest are more robust in body form therefore elongate-narrow form is likely apotypic.

2. Pronotum with scale pattern slightly to distinctly vittate, with white scales largest and/or densest immediately laterad of midline, smaller and/or sparser laterally; largely whitish in color, the underlying dark cuticle largely obscured by the white scales (Figs. 118–136). This state is present in *Lixoglyptus* and *Cleonidius* species as well as *Pseudocleonus*, *Mecaspis*, and various other species of *Lixus*. A distinct pronotal scale pattern is lacking from many genera including *Cylindropterus*.

3. Eye elongate-oval in shape. This state is found in the three genera in question as well as numerous other genera of Cleoninae. Polarity of the states of this character has not been determined.

4. Eye more or less flat in dorsal view. This state is found in the three taxa in question as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

5. Tibiae with corbel ridge rounded (as in Fig. 5). This state is present in the three taxa in question, *Lixocleonus*, *Menocleonus*, *Epirhynchus*, and all *Lixus* species. Polarity of the states of this character has not been determined.

6. Tarsi with articles moderately wide, not markedly elongate-narrow. This state is found in the three taxa in question as well as numerous other Cleoninae. Molytinae of interest also possess this state and thus it is likely plesiotypic.

7. Tarsi with ventral pilose pads present, large and distinctly delimited. This state is found in the three taxa in question as well as numerous other Cleoninae. Molytinae of interest also

possess this state and thus it is likely plesiotypic.

8. Pronotum with dorsal surface punctate, not tuberculate. This state is found in the taxa in question as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

9. Female with spermathecal gland spherical, not elongate and cylindrical. This state is found in the three taxa in question as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

10. Rostrum moderately to very elongate-narrow. This state is found in the three taxa in question (although not all species of *Cleonidius*) as well as various other Cleoninae. Polarity of the states of this character has not been determined.

11. Pronotum with postocular lobes present. This state is found in the three taxa in question (although not in all species of *Cleonidius*) as well as numerous other Cleoninae. Molytinae of interest also possess this state and thus it is likely plesiotypic.

12. Female with abdominal sternum VIII with basal arm present, short to long (Figs. 113–114, 157–176). This state is found in the three taxa in question as well as in numerous other genera of Cleoninae. Molytinae of interest possess a long basal arm and thus this state is likely plesiotypic with a successively shorter arm increasingly apotypic.

13. Antenna with apical three articles with placoidal sensillae lacking or else very few in number. This state is found in the three genera in question as well as *Lixocleonus* and *Lixus* species. Polarity of states of this character has not been determined and not all Cleoninae have been examined in detail for this character.

14. Prosternum with swelling in front of fore-coxal cavity. This state is found in the three taxa in question and *Cosmogaster, Mecaspis, Lixocleonus, Microcleonus* and *Lixus*. Polarity of states of this character has not been determined.

Genus *Apleurus* Chevrolat

Character evolution

Character state 1 for each character is considered plesiotypic; other states are considered apotypic at various levels (see Table I).

Primary characters

Character 1. Epistoma, apical margin.— Two states of this character are recognized:

1. emarginate (Fig. 81b);
2. rounded and produced (Figs. 82b–88b).

Out-groups, most Cleoninae, and Molytinae possess an emarginate epistoma. An apically rounded epistoma is otherwise known only in *Gonocleonus, Leucochromus, Eurycleonus*, and *Koenigius*.

Character 2. Prementum, setae.— Two arbitrarily defined states of this character are recognized:

1. lacking or with only one large seta per side (Figs. 61–62);
2. with two or more large setae per side (Fig. 63).

Out-groups *Cnemodontus* and *Chromoderus* lack and possess one large seta per side respectively. Other Cleoninae were not examined in detail for this character, however, at least some species of *Lixus* and *Cleonidius* possess two or more long setae on each side of the prementum.

Character 3. Pronotum, tubercles, development and shape of anterior angles.— Three states are recognized:

1. absent (Figs. 24, 68–69);

2. present, anterior angles obtuse (Figs. 75–80);

3. present, anterior angles acute (Figs. 70–74).

Out-groups lack distinct tubercles but the pronota are slightly constricted at the apical one-third to one-quarter, the position of the tubercles if developed. This and lack of acutely-angled tubercles in other Cleoninae which possess variously developed pronotal tubercles, justify recognition of obtusely angled tubercles as plesiotypic.

Character 4. Tarsus, ventral pilose vestiture.— Three arbitrarily defined states are recognized:

1. extensive;

2. moderately reduced in extent;

3. markedly reduced in extent, or absent.

Out-groups each possess extensive ventral tarsal pilose vestiture. This state is considered plesiotypic and successive stages in reduced extent of pilose vestiture increasingly apotypic. Molytinae possess extensive ventral pilose vestiture. Extent of ventral tarsal pilose vestiture varies extensively in Cleoninae and on that basis alone this character should perhaps best be regarded as of a secondary nature. However, compatibility of successively apotypic states of this character with numerous other primary characters results in increased confidence that it also be considered primary.

Character 5. Female, stylus, size.— Three states are recognized:

1. large (Figs. 89b-91b);

2. small (Figs. 92b-94b);

3. absent (Figs. 95b-96b).

Out-groups and all Cleoninae examined (except for *Brachycleonus* in which a stylus is absent) possess a moderately large stylus. Decreased size is considered increasingly apotypic.

Character 6. Female, stylus, position.— Three states are recognized:

1. apical (Figs. 89b-91b);

2. anteapical (Figs. 92b-94b);

3. absent, anteapical sclerotized ridge present (Figs. 95b-96b).

Out-groups and all Cleoninae examined in which a stylus is present, possess an apically situated stylus. The anteapical sclerotized ridge is regarded as positionally homologous with the stylus in other *Apleurus* species and thus state 3 is not considered as increasingly apotypic.

Character 7. Male, abdominal sternum VII, dorsally directed tooth at apical margin.— Two states are recognized:

1. absent;

2. present.

Out-groups and all Cleoninae except *Brachycleonus* and *Centrocleonus* lack a dorsally directed tooth on the apical margin of abdominal sternum VII.

Character 8. Male, abdominal sternum VIII, interior angles of each sternite.— Three states are recognized:

1. basal projection absent (Fig. 97f);

2. basal projection slightly to moderately developed (Fig. 101e);

3. basal projection present, markedly developed (Fig. 103e).

Both out-groups lack a basal projection. Extent of development from slight to marked represents successively apotypic states. Other Cleoninae have not been examined in detail for this character although a distinct basal projection is lacking from both *Cleonidius* and *Stephanocleonus*.

Secondary characters

Character 9. Size, length of elytra.— Three arbitrarily defined states are recognized (Fig. 105).
1. X<7.0 mm;
2. 7.0 mm<X<9.0 mm;
3. X>9.0 mm.

Large size (state 3) is widespread in Cleoninae but the out-groups *Chromoderus* and *Cnemodontus* possess state 1 and state 2 respectively. Small size of *Chromoderus* and primitive *Apleurus* species, however, suggests that the common ancestor of *Chromoderus* and *Apleurus* was also of small size, and that medium to large sizes (states 2 and 3) in *Apleurus* are successively apotypic. Whether the medium size of *Chromoderus* is then primitive or represents an independent increase in size is not known.

Character 10. Eye, prominence and convexity.— Three arbitrarily defined states are recognized:
1. markedly convex and prominent;
2. slightly to moderately prominent and convex;
3. flat.

Flat, non-prominent eyes are known in virtually all Cleoninae with the exception of *Lixocleonus*, *Microlarinus*, and various *Lixus* species. Out-groups *Cnemodontus* and *Chromoderus* have markedly convex and flat eyes respectively. As for character 9, occurrence of markedly convex eyes in one of the out-groups and in primitive species of *Apleurus*, suggests that this state is plesiotypic. Decreased prominence and convexity of eyes is thus considered apotypic.

Character 11. Suberect or erect vestiture, length.— Three states are recognized:
1. absent or indistinct;
2. short;
3. long.

Out-groups lack distinct erect vestiture. Presence and subsequently increased length of vestiture are considered successively apotypic. Long suberect or erect vestiture is known in numerous genera of Cleoninae and other Curculionidae (*e.g.,* Trigonoscuta, Miloderes, *etc.*) and appears correlated with life in sand substrates.

Character 12. Rostrum, carina.— Two states are recognized:
1. present (Figs. 84–86);
2. absent (Figs. 81–83, 87–88).

Both out-groups possess a rostral carina. However, primitive *Apleurus* species lack a carina. This suggests that lack of a carina is apotypic for *Apleurus* but that presence of a carina in certain species of *Apleurus* is also apotypic.

Character 13. Rostrum, declivity at apex.— Two states are recognized:
1. flat to at most slightly declivous (Figs. 81a-83a);
2. moderately to steeply declivous (Figs. 84a-88a).

Out-groups possess a flat to slightly declivous rostral apex. A rostrum with a steeply declivous apex also occurs in many other Cleoninae.

Character 14. Maxillary palpus, setae.— Two states are recognized:
1. one large seta on palpifer, one on stipes (Fig. 64);
2. one large seta on palpifer (Fig. 65).

Out-groups possess large setae on both palpifer and stipes. Whether this seta is lacking or simply reduced in size was not determined. Other Cleoninae were not examined in detail for this character.

Character 15. Pronotum, width.— Two states are recognized (see Fig. 109):
1. width greatest at base to width at base more or less subequal to width at tubercles;
2. width distinctly greatest at tubercles.

Out-groups have pronota that are widest at the base. Pronota that are distinctly widest at the tubercles are also known in *Tetragonothorax* and *Gonocleonus.*

Character 16. Pronotum, punctation.— Two states are recognized:
1. small and shallow;
2. large and deep.

Out-groups have pronota that have small shallow punctures. No other Cleoninae examined have similarly large and deep pronotal punctures.

Character 17. Pronotum, median carina.— Two states are recognized:
1. absent;
2. present, of variable extent.

Out-groups lack a pronotal carina. Presence of a carina is widespread and common in most genera of Cleoninae.

Character 18. Prosternum, impressions and swellings.— Four arbitrarily defined states are recognized in this lineage:
1. impression anterolaterad of fore-coxal cavity present; no swelling present;
2. impression anterolaterad of fore-coxal cavity present; swelling immediately anterior to impression present, low and rounded (Figs. 82a-83a);
3. impression anterolaterad of fore-coxal cavity present; swelling immediately anterior to impression present, high (Figs. 81a, 84a-88a);
4. impression anterolaterad of fore-coxal cavity present; swelling immediately anterior to impression present, low and rounded; low rounded swelling also present immediately in front of fore-coxal cavity.

All Cleoninae possess an impression, although various in depth and extent, immediately anterolaterad of each fore-coxal cavity. Swellings, if present, are found in two locations, one, immediately in front of the fore-coxal cavity, adjacent to the impression, or two, immediately in front of the impression. Out-group *Cnemodontus* lacks swellings and *Chromoderus* is unique in Cleoninae examined in that it has swellings in front of both the fore-coxal cavity and the impression. Primitive *Apleurus* have low rounded swellings anterior to the impression, thus this state is judged plesiotypic for *Apleurus*; high swellings in front of the prosternal impressions are considered apotypic. Swellings in front of the impression are widespread in Cleoninae but are generally low and rounded except in *Stephanocleonus* and *Conorhynchus*. They are however absent from most genera. *Cosmogaster, Mecaspis, Lixocleonus, Microcleonus, Lixus* and *Cleonidius* all have a swelling of variable extent in front of the fore-coxal cavity.

Character 19. Elytra, elevation of intervals.— Two states are recognized;
1. all intervals equally flat or only slightly elevated and convex;

2. sutural interval and intervals 3, 5, 7, and 9 slightly to markedly elevated and convex.

Out-groups possess state 1. The apotypic state occurs in many genera of Cleoninae and other Curculionidae. Development of elevated and convex elytral intervals appears to be correlated with reduction in size or absence of the metathoracic wings.

Character 20. Fore-tibia of female, apex.— Two states are recognized:

1. uncus and large subapical tooth present;
2. uncus and at most only small subapical tooth present.

Out-groups each possess a large tooth in addition to the uncus. Both states are widespread in Cleoninae.

Character 21. Fore-tibia, inner margins.— Two states are recognized:

1. large denticles present;
2. with at most only small denticles present.

Cnemodontus individuals possess large fore-tibial denticles; *Chromoderus* individuals, only small denticles. Both states are widespread in other Cleoninae.

Character 22. Female abdominal sternum VIII, lateral arms.— Two states are recognized:

1. more or less straight throughout length (Figs. 49e-50e, 90b-91b, 95b-96b);
2. arcuate (Figs. 89b, 92b-94b).

Abdominal sternum VIII in females of both out-groups has lateral arms that are more or less straight. Both states are widespread in Cleoninae.

Character 23. Female abdominal tergum VII, median longitudinal carina.— Three states are recognized:

1. absent;
2. slightly developed;
3. markedly developed.

Cnemodontus lacks a longitudinal carina whereas a markedly developed carina is present in *Chromoderus*. Other Cleoninae examined lack a carina.

Character 24. Female abdominal tergum VIII, median longitudinal carina.— Three states are recognized:

1. absent;
2. slightly developed;
3. markedly developed.

Cnemodontus lacks a longitudinal carina whereas a slightly developed carina is present in *Chromoderus*. Other Cleoninae examined lack a carina.

Character 25. Male, aedeagus, curvature.— Two states are recognized:

1. markedly arcuate at base (Figs. 56a-57a);
2. more or less evenly arcuate throughout length (Figs. 97d, 98c-104c).

Both out-groups possess an aedeagus that is markedly arcuate at the base. Both states occur in *Stephanocleonus* (Ter-Minasyan 1979). The aedeagus of all *Cleonidius* species, *Lixoglyptus* and *Cylindropterus* is evenly arcuate throughout its length. Other Cleoninae have not been examined in detail for this character.

Character 26. Male, aedeagus, apex.— Two states are recognized:

1. spatulate (Figs. 56a-57a);
2. not spatulate (Figs. 97d, 98c-104c).

Both out-groups possess an aedeagus with a spatulate apex. Both states are widely distributed in Cleoninae.

Character 27. Male, aedeagus, internal sac, paired lateral sclerite at midlength.— Two states are recognized:
1. present (Fig. 57b);
2. absent (Figs. 56b, 97a-104a).

Cnemodontus males possess a distinct paired lateral sclerite at the midlength of the internal sac; *Chromoderus* males lack such sclerites. *Stephanocleonus, Prionorhinus,* and *Lixomorphus* males also possess such sclerites, and another unpaired sclerite, situated in a ventral position closer to the apex of the internal sac, is present in *Menocleonus, Pleurocleonus,* and *Xanthochelus.* This latter sclerite, however, is questionably homologous with the paired sclerite at midlength.

Character 28. Male, aedeagus, internal sac, shape.— Two states are recognized:
1. dorsal median pocket low and with two pairs of lobes (Figs. 56b-57b, 97a-99a);
2. dorsal median pocket high and with one pair of lobes (Figs. 100a-104a).

Cnemodontus males possess an internal sac with state 1; *Chromoderus* males possess an internal sac with state 2. The shape of the internal sac varies in other Cleoninae examined, but only in some species of *Cleonidius* is it similarly high and possessing of only a single pair of lobes.

Character 29. Male, aedeagus, internal sac, lobe A.— Two states are recognized:
1. present (Figs. 56b,c-57b,c);
2. absent (Figs. 97a,b-104a,b).

Males of each out-group possess lobe A. This character has not been examined in detail in other Cleoninae. However, lobe A is present in at least *Cleonidius, Lixoglyptus, Cylindropterus, Adosomus, Cleonis* and *Cyphocleonus.* It is absent from those *Stephanocleonus* examined.

Character 30. Male, aedeagus, internal sac, apical sclerite complex, median projection.— Two states are recognized:
1. long (Figs. 56d-57d, 103d-104d);
2. absent or present, but short and indistinct (Figs. 97c, 98d-101d).

Both *Cnemodontus* and *Chromoderus* males possess apical sclerite complexes with a well-developed median projection. Presence of state 2 in primitive *Apleurus* species suggests presence of state 1 within *Apleurus* is secondarily apotypic. This character has not been examined in detail in other Cleoninae.

Character 31. Male, aedeagus, internal sac, apical sclerite complex, sclerotization of base and sides of the apical pocket.— Two states are recognized:
1. well-sclerotized, dark brown in color;
2. lightly-sclerotized, pale brown in color.

Males of each out-group have the base and sides of the apical pocket markedly sclerotized. This character has not been examined in detail in other Cleoninae.

Table I. Plesiotypic and apotypic states of characters used in phylogenetic analysis of *Apleurus* species and related taxa

Character	Plesiotypic	Apotypic
1. Epistoma, apical margin	—emarginate	—rounded and produced
2. Prementum, setae	—setae lacking or only one large seta per side	—2 or more large setae per side
3. Pronotum, tubercles, development and shape of anterior angles	—tubercles absent	—tubercles present, anterior angles obtuse (2) —tubercles present, anterior angles acute (3)
4. Tarsus, ventral pilose vestiture	—present, extensive	—present, moderately reduced in extent (2) —present, markedly reduced in extent or absent (3)
5. Female, stylus, size	—present, large	—present small (2) —absent (3)
6. Female, stylus, position	—present, apical	—present, anteapical (2) —absent, anteapical sclerotized ridge present (3)
7. Male, abdominal sternum VII, dorsally directed tooth at apical margin	—absent	—present
8. Male, abdominal sternum VIII, interior angles of each sternite	—basal projection absent	—basal projection present, slightly to moderately developed (2) —basal projection present, markedly developed (3)
9. Size, length of elytra	—X < 7.0 mm	—7.0 mm < X < 9.0 mm (2) —X > 9.0 mm (3)
10. Eye, prominence and convexity	—markedly convex and prominent	—slightly to moderately prominent and convex (2) —flat (3)
11. Suberect or erect vestiture, length	—absent or indistinct	—present, short (2) —present, long (3)
12. Rostrum, carina	—present	—absent
13. Rostrum, declivity at apex	—flat to slightly declivous	—moderately to steeply declivous
14. Maxillary palpus, setae	—one large seta on palpifer, one on stipes	—one large seta on palpifer
15. Pronotum, width	—greatest at base to subequal at base and tubercles	—greatest at tubercles

Table I (continued)

Character	Plesiotypic	Apotypic
16. Pronotum, punctation	—small and shallow	—large and deep
17. Pronotum, median carina	—absent	—present, various in extent
18. Prosternum, impressions and swellings	—impression anterolaterad of fore-coxal cavity; no swelling present	—impression anterolaterad of fore-coxal cavity; low rounded swelling present immediately anterior to impression (2) —impression anterolaterad of fore-coxal cavity; high sharp swelling present immediately anterior to impression (3) —impression anterolaterad of fore-coxal cavity; low rounded swelling present immediately anterior to impression and low rounded swelling present immediately in front of fore-coxal cavity (4)
19. Elytra, elevation of intervals	—all intervals equally flat or slightly elevated and convex	—sutural and intervals 3, 5, 7, and 9 slightly to markedly elevated and convex
20. Fore-tibia of female, apex	—uncus and large subapical tooth present	—uncus and at most small subapical tooth present
21. Fore-tibia, inner margins	—large denticles present	—small denticles present
22. Female abdominal sternum VIII, lateral arms	—more or less straight throughout length	—arcuate
23. Female abdominal tergum VII, median longitudinal carina	—absent	—present, slightly developed (2) —present, markedly developed (3)
24. Female abdominal tergum VIII, median longitudinal carina	—absent	—present, slightly developed (2) —present, markedly developed (3)
25. Male, aedeagus, curvature	—markedly arcuate at base	—more or less evenly arcuate throughout length
26. Male, aedeagus, apex	—spatulate	—not spatulate

Table I (continued)

Character	Plesiotypic	Apotypic
27. Male, aedeagus, internal sac, paired lateral sclerite at midlength	—present	—absent
28. Male, aedeagus, internal sac, shape	—dorsal median pocket low, two pairs of lobes	—dorsal median pocket high, one pair of lobes
29. Male, aedeagus, internal sac, lobe A	—present	—absent
30. Male, aedeagus, internal sac, apical sclerite complex, median projection	—present, long	—present, short and indistinct or absent
31. Male, aedeagus, internal sac, apical sclerite complex, sclerotization of base and sides or apical pocket	—well-sclerotized, dark brown in color	—lightly-sclerotized, pale brown in color

Table II. Character states in *Apleurus* species and related taxa

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
A. hystrix	1	1	1	1	2	1	1	1	1	1	3	2	1	2	1	2	1	2	1	2	2	2	1	1	2	1	2	2	2	2	2
A. aztecus	2	1	1	2	1	1	1	1	1	1	1	2	1	2	1	1	1	2	2	1	2	1	1	1	2	2	2	1	2	2	1
A. lutulentus	2	1	1	2	1	1	2	2	2	1	1	2	1	1	1	1	1	2	1	2	2	1	1	1	2	2	2	1	2	2	1
A. porosus	2	2	2	3	2	2	2	2	1	1	1	1	2	2	1	2	1	3	2	2	2	2	1	1	2	2	2	2	2	2	2
A. angularis	2	2	3	3	2	2	2	2	3	1	3	1	2	2	2	2	1	3	2	2	2	2	1	1	2	2	2	2	2	2	2
A. jacobinus	2	2	3	3	3	2	2	2	1	2	3	1	2	2	2	2	2	3	2	2	2	2	1	1	2	3	2	2	2	2	2
A. albovestitus	2	2	2	3	3	3	3	3	3	2	1	2	2	1	1	1	2	3	1	2	2	1	2	3	2	3	2	2	2	1	1
A. saginatus	2	2	2	3	3	3	2	3	3	2	1	2	2	1	1	1	2	3	1	2	2	1	2	3	2	2	2	2	2	1	1
Chromoderus	1	1	1	1	1	1	1	1	1	3		1	1	1	1	1	1	1	1	1	2	1	3	2	1	1	2	2	1	1	1
Cnemodontus	1	1	1	1	1	1	1	1	2	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Phylogenetic relationships of included species

Distribution of character states is shown in Table II.

Confidence in phylogenetic relationships of species of *Apleurus* (Figs. 234–235) is high; most primary characters exhibit very little homoplasy elsewhere in Cleoninae and the distribution of apotypic states is concordant with distributions of apotypic states in most secondary characters. Furthermore, primary characters are employed to define most major lineages and are more general in their applicability (Fig. 234) (*i.e.,* not all primary characters are used to define the same or few lineages). Because of this, confidence in recognizing homoplasy in secondary characters is enhanced and their applicability amplified.

Relationships among *Chromoderus, Cnemodontus* and *Apleurus* based on primary characters are unclear (Fig. 234). Apotypic states of secondary characters of size of female fore-tibial denticles, and presence or absence of a paired lateral sclerite at midlength in the internal sac of the aedeagus of males, suggests *Chromoderus* is the sister group to *Apleurus*, with *Cnemodontus* as sister to the *Chromoderus-Apleurus* lineage (Fig. 235). Flat eyes in *Chromoderus* and most other Cleoninae, and shared presence of swollen and convex eyes in *Cnemodontus* and most *Apleurus* is the only evidence that *Cnemodontus* is sister to *Apleurus*. However, I favour consideration of flat eyes as independently derived in *Chromoderus* and swollen and convex eyes as plesiotypic for the lineage.

Monophyly of *Apleurus* is based upon distribution of apotypic states of a number of characters, both primary and secondary. All *Apleurus* have ventral tarsal pilose vestiture moderately to markedly reduced in extent, the aedeagus of males is evenly arcuate throughout its length, the apex of the aedeagus is not spatulate, and the internal sac of the aedeagus lacks lobe A. These apotypic states all occur elsewhere in Cleoninae but not in those taxa believed closely related to *Apleurus*. Although there is homoplasy within *Apleurus*, distributions of apotypic states of other characters also support monophyly of the genus. These states are lack of a rostral carina (secondarily derived in *A. angularis-A. jacobinus-A. porosus* lineage), fore-tibia of female with small subapical second spur (secondarily derived in *A. aztecus*), and internal sac of aedeagus of male with the median projection of the apical sclerite complex absent or short and indistinct (secondarily derived in *A. albovestitus-A. saginatus* lineage).

Apleurus (Gibbostethus) hystrix is hypothesized to be the most primitive species of *Apleurus* (Figs. 234–235). It is the only species of *Apleurus* which has an emarginate epistoma; all other *Apleurus* species have the epistoma rounded. *Apleurus hystrix* is autapotypic in a number of characters (see species treatment of *A. hystrix*), and also shares, with various other species of *Apleurus*, a number of apotypic states which are best regarded as homoplasious. All of these apotypic states are of secondary characters and are otherwise found only in the *A. angularis-A. jacobinus-A. porosus* lineage or the common ancestor of this lineage and the *A. albovestitus-A. saginatus* lineage. This suggests that *A. hystrix* might be better placed with these species, but distribution of apotypic states of all primary characters in the analysis argues against this proposal (Fig. 234).

Apleurus aztecus is the next most primitive species and is sister to the remainder of the subgenus *Apleurus* (Figs. 234–235). Phylogenetic position of this species is based upon possession of a rounded epistoma, lack of a dorsally directed tooth at the apical margin of abdominal sternum VII in males, and lack of basal projections on the interior angles of each sternite of abdominal sternum VIII also in males.

Apleurus lutulentus is sister to the ancestor of the *A. angularis-A. jacobinus-A. porosus* and *A. albovestitus-A. saginatus* lineages (Figs. 234–235). This position is due to distributions

of apotypic states of numerous primary as well as secondary characters. These latter five species comprise a monophyletic group divisible into two lineages as noted above. Monophyly of the *A. angularis-A. jacobinus-A. porosus* lineage is based upon possession of acute-angled pronotal tubercles, presence of rostral carina, maxillary palpus with only one large seta on palpifer, large and deep pronotal punctation, alternate elytral intervals elevated and convex, female abdominal sternum VIII with arcuate lateral arms, female abdominal tergum VIII with slight median longitudinal carina, and internal sac of aedeagus of male with sides and base of apical pocket only lightly sclerotized. Within this group of species, long erect dorsal vestiture and relative width of the basal and apical portions of the pronotum suggests an *A. angularis-A. jacobinus* sister species relationship. Widely divergent tarsal claws in all *A. angularis* and some *A. porosus* are likely a result of independent evolution or of hybridization.

The sister species status of *A. albovestitus* and *A. saginatus* (Figs. 234–235) is strongly supported by the lack of a stylus on gonocoxite II of the female and by markedly developed basal projections on the interior angles of each sternite of abdominal sternum VIII in males. Distribution of apotypic states of numerous secondary characters supports this relationship.

Alternative hypotheses

The only apparent possible alternative hypothesis of phylogenetic relationship to that presented in Figure 235 concerns the placement of *Apleurus hystrix*. Although primary characters indicate a primitive phylogenetic position for this species, there are a number of secondary character states homoplasious with the *A. porosus-A. jacobinus-A. angularis* lineage which could be interpreted as suggesting inclusion in that lineage.

Genus *Cleonidius* Casey

Character evolution

Character state 1 for each character is considered plesiotypic; other states are considered apotypic at various levels (see Table III).

Primary characters

Character 1. Submentum, degree of ventral swelling.— Two states of this character are recognized:
1. flat, not ventrally swollen (Figs. 137a-142a, 145a-156a);
2. swollen ventrally (Figs. 143a-144a).
    Out-groups and all Cleoninae examined possess a submentum that is not swollen ventrally.
    Character 2. Rostrum, ratio of length to width in females.— Four arbitrarily defined states are recognized (see Fig. 198):
-1. very elongate, $X<0.45$ (Fig. 141);
1. moderately elongate, $0.45<X<0.65$ (Figs. 137–140, 142–144, 148–155);
2. short, robust, $0.65<X<0.77$ (Figs. 145, 156);
3. very short, very robust, $X>0.77$ (Figs. 146–147).
    Out-groups possess a rostrum that is moderately elongate. Successively shorter and more robust rostra are considered increasingly apotypic. A very elongate rostrum is also considered apotypic. States of this character are widely distributed in Cleoninae although in general members of the tribe Lixini possess a more elongate, narrow rostrum than do members of the Cleonini. Rostral length in Molytinae of phylogenetic interest varies from moderately to very elongate.

Character 3. Rostrum, degree of lateral swelling.— Two states are recognized:

1. not swollen at midlength in dorsal view (Figs. 137b-142b, 145b-156b);
2. swollen at midlength in dorsal view (Figs. 143b-144b).

Out-groups possess state 1. No other Cleoninae or Molytinae of phylogenetic concern examined possess a similarly laterally expanded rostrum.

Character 4. Frons/vertex, surface sculpture.— Three states of this character are recognized:

1. area behind eye with wrinkles of cuticle;
2. area behind eye with a curved sulcus (Fig. 150a);
3. area behind eye with a deep, straight sulcus (Fig. 139).

Other than various punctures, out-groups and most Cleoninae possess at most only a few wrinkles of the cuticle behind the eye. Some African *Lixus* possess a very deep elongate impression above the eye. State 3 is unlikely homologous with states 1 and 2.

Character 5. Elytra, scale pattern.— Three states of this character are recognized:

1. marginal; intervals 9 to 11 with dense, moderately large, white scales, otherwise moderately densely and uniformly covered with fine white scales which are smaller than those on intervals 9 to 11 (Figs. 118–123);
2. vittate; intervals other than 9 to 11 with scales as large as those on intervals 9 to 11 (Figs. 127–128, 130–136);
3. mottled; with irregularly scattered and sized patches of large white scales (Figs. 124–126, 129).

Of the out-groups, *Cylindropterus* lacks a distinct scale pattern whereas *Lixoglyptus* species both have elytral scale patterns that are of the marginal type. Most *Lixus* species possess uniformly dense small fine scales on the elytra although elytra of individuals of a few species are distinctly vittate. Members of the Cleonini have various elytral scale patterns, but these are not recognizable as any of the states discussed herein for *Cleonidius*. State 1 is considered plesiotypic based largely on its occurrence in *Lixoglyptus* species. This state is assumed to represent an intermediate stage between the uniformly distributed small fine scales of most *Lixus* and the vittate state of certain *Cleonidius* species. The mottled state is then assumed to be a result of decreased scale size at various positions of the vittate pattern and is homoplasious within *Cleonidius* although restricted to a single species group.

Character 6. Abdomen of female, ornamentation of abdominal sternum VII.— Two states of this character are recognized:

1. basal margin uniformly flat;
2. basal margin at middle internally (dorsally) with variously developed glabrous shiny tubercle.

Out-groups and all other Cleoninae examined possess state 1. Within *Cleonidius* there is variation within and between species in the degree of development of the tubercle. Very slightly developed tubercles or glabrous patches are also present at the basal margin of abdominal sterna V and VI in some specimens, but in these individuals, the most markedly developed tubercle is that on sternum VII.

Character 7. Male, aedeagus, internal sac, height of dorsal median pocket.— Two states of this character are recognized:

1. low (Figs. 111a-112a, 177a-179a, 183a-196a);
2. high (Figs. 180a-182a).

Out-groups possess a low dorsal median pocket. Both states occur elsewhere in Cleoninae but the character has not been examined in detail.

Character 8. Male, aedeagus, internal sac, apex of dorsal median pocket.— Two states of this character are recognized:

1. rounded or truncate in dorsal view (Figs. 111b-112b, 177b-191b, 196b);
2. emarginate or sinuate in dorsal view (Figs. 192b-195b).

Out-groups possess a dorsal median pocket with a rounded to truncate apical margin. Other Cleoninae have not been examined in detail for this character.

Character 9. Male, aedeagus, internal sac, lobe B.— Two states of this character are recognized:

1. present (Figs. 111a-112a, 177a-179a, 183a-196a);
2. absent (Figs. 180a-182a).

Out-groups possess a lobe B on the internal sac. Other Cleoninae have not been examined in detail for this character although both states are found in *Apleurus* species, *Cleonis* and *Cnemodontus* possess a lobe B, and the lobe is lacking from *Stephanocleonus* species examined and *Chromoderus*.

Character 10. Male, aedeagus, internal sac, lobe D.— Two states of this character are recognized:

1. present (Figs. 111a-112a, 177a-179a, 183a-196a);
2. absent (Figs. 180a-182a).

The internal sac of each out-group possesses a lobe D, however, the lobe is small in *L. spartii*. Lobe D is present in all species of *Apleurus*, *Cleonis*, *Stephanocleonus*, *Chromoderus*, and *Cnemodontus* examined.

Secondary characters

Character 11. Size, length of elytra.— Two arbitrarily defined states of this character are recognized (see Fig. 197):

1. large, $X > 9mm$;
2. small, $X < 9mm$.

Individuals of both out-groups are large in size but distribution of states of primary characters within *Cleonidius* suggests large size of some *Cleonidius* species is secondarily apotypic. Within and between species variation in size is extensive in most Cleoninae.

Character 12. Rostrum, punctation.— Two states are recognized:

1. apical portion with punctures moderately dense and moderately deep;
2. apical portion with punctures sparse, small and shallow.

Out-groups each possess state 1. State 2 occurs in most species of *Lixus* and appears associated with an elongate-narrow rostrum. The apotypic state of this character is homoplasious within *Cleonidius*.

Character 13. Rostrum, median tumescence.— Three states are recognized:

1. absent (Figs. 139b, 141b-142b, 152b);
2. present, slightly developed (Figs. 140b, 143b-144b, 146b-149b);
3. present, markedly developed (Figs. 137b-138b, 145b, 150b-151b, 153b-156b).

Out-groups each possess state 1. Increased degree of development of the median tumescence is considered increasingly apotypic. There is extensive homoplasy in this character.

Character 14. Rostrum, lateral margins.— Two states are recognized:

1. rounded;

2. sharp.

Out-groups each possess state 1. Species of *Lixus* and *Larinus* examined possess rounded lateral margins; species of Cleonini have either state.

Character 15. Pronotum, anterolateral margins.— Three states are recognized:

1. postocular lobe rounded, well-developed (Figs. 137a-139a, 141a-144a, 146a-151a);
2. postocular lobe rounded, slightly developed (Figs. 140a, 152a);
3. postocular lobe absent, margin straight (Figs. 145a, 153a-155a).

Out-groups and most other Cleoninae possess well-developed postocular lobes. Successively less markedly developed postocular lobes are increasingly apotypic. Acute pronotal postocular projections, although present in some Cleoninae which lack rounded postocular lobes (*e.g.*, *Lixus*, *Apleurus*), are not present in those *Cleonidius* species that lack a postocular lobe. This character is homoplasious in *Cleonidius*.

Character 16. Pronotum, impressions.— Two states are recognized:

1. basal median area shallowly to moderately deeply impressed;
2. basal median area deeply impressed, lateral margins variously longitudinally impressed.

State 1 occurs in both out-groups. Similar sculpture is not present in other Cleoninae examined.

Character 17. Suberect or erect vestiture, length.— Three states are recognized:

1. absent (Figs. 140a, 152a, 156a);
2. present, short to moderate in length (Figs. 138a-139a, 145a-149a, 151a, 153a);
3. present, long (Figs. 137a, 141a-144a, 150a, 154a-155a).

Both out-groups and many *Lixus* lack suberect or erect vestiture. Increased length of vestiture is considered as increasingly apotypic. There is extensive homoplasy in this character in *Cleonidius* and in Cleoninae in general.

Character 18. Tarsus, ventral pilose vestiture.— Three states are recognized:

1. extensive;
2. moderately reduced in extent;
3. markedly reduced in extent, to absent.

Both out-groups, all *Lixus* species examined, many Cleonini, and Molytinae possess extensive ventral pilose vestiture. Successive stages in reduction of vestiture are considered as increasingly apotypic. Reduced ventral pilose vestiture is otherwise confined to members of Cleonini. This character is homoplasious in *Cleonidius*.

Character 19. Foretibia of female, inner margin.— Two states are recognized:

1. large denticles present (as in Fig. 144c);
2. only small denticles present (as in Fig. 143c).

Both out-groups possess large denticles on the inner margin of the foretibia. Distribution of states of primary characters within *Cleonidius* suggests presence of large denticles in some species of *Cleonidius* is secondarily apotypic and homoplasious. Both states of this character occur in other Cleoninae.

Character 20. Female abdominal sternum VIII, length of basal arm.— Two states are recognized:

1. long (Figs. 165, 167–169, 174);
2. short (Figs. 157–164, 166, 170–174, 175–176).

Out-groups each possess a long basal arm. Both states of this character are widely distributed in Cleoninae, but as Molytinae examined possess a long basal arm, this state is likely plesiotypic for Cleoninae. This character is homoplasious in *Cleonidius*.

Character 21. Female abdominal sternum VIII, shape of lateral arms.— Two states are recognized:
1. arcuate (Figs. 163, 165–175);
2. more or less straight, divergent (Figs. 157–162, 164, 176).

Out-groups each possess state 1. This character is homoplasious in *Cleonidius*. Both states occur in other Cleoninae.

Character 22. Male, aedeagus, internal sac, lobe E.— Two states are recognized:
1. present (Figs. 111a, 177a-179a, 183a-196a);
2. absent (Figs. 112a, 180a-182a).

The internal sac of *Cylindropterus* possesses a lobe E; that of *Lixoglyptus* lacks lobe E. Lobe E is present in species of *Cleonis*, *Cnemodontus*, some *Apleurus* and at least some *Stephanocleonus*. Distribution of states of primary characters within *Cleonidius* suggests presence of lobe E be considered plesiotypic.

Table III. Plesiotypic and apotypic states of characters used in phylogenetic analysis of *Cleonidius* species and related taxa

Character	Plesiotypic	Apotypic
1. Submentum, degree of ventral swelling	—flat	—swollen
2. Rostrum, ratio of length to width	—moderately elongate, $0.45 < X < 0.65$	—very elongate, $X < 0.45$ (-1) —short, robust, $0.65 < X < 0.77$ (2) —very short, robust, $X > 0.77$ (3)
3. Rostrum, degree of lateral swelling	—not swollen at midlength	—swollen at midlength
4. Frons/vertex, surface sculpture	—area behind eye with wrinkles of cuticle	—area behind eye with curved sulcus (2) —area behind eye with deep, straight sulcus (3)
5. Elytra, scale pattern	—marginal (see text)	—vittate (see text) (2) —mottled (see text) (3)
6. Abdomen of female, ornamentation of abdominal sternum VII	—basal margin uniformly flat	—basal margin at middle internally with variously developed glabrous shiny tubercles
7. Male, aedeagus, internal sac, height of dorsal median pocket	—low	—high
8. Male, aedeagus, internal sac, apex of dorsal median pocket	—rounded or truncate in dorsal view	—emarginate or sinuate in dorsal view
9. Male, aedeagus, internal sac, lobe B	—present	—absent
10. Male, aedeagus, internal sac, lobe D	—present	—absent
11. Size, length of elytra	—$X > 9$ mm	—$X < 9$ mm
12. Rostrum, punctation	—apical portion with punctures moderately large, dense and moderately deep	—apical portion with punctures sparse, small and shallow
13. Rostrum, median tumescence	—absent	—present, slightly developed (2) —present, markedly developed (3)
14. Rostrum, lateral margins	—rounded	—sharp

Table III (continued)

Character	Plesiotypic	Apotypic
15. Pronotum, anterolateral margins	—postocular lobe rounded, well-developed	—postocular lobe rounded, slightly developed (2) —postocular lobe absent, margin straight (3)
16. Pronotum, impressions	—basal median area shallowly to moderately deeply impressed	—basal median area deeply impressed, lateral margins variously longitudinally impressed
17. Suberect or erect vestiture, length	—absent	—present, short to moderate (2) —present, long (3)
18. Tarsus, ventral pilose vestiture	—present, extensive	—present, moderately reduced (2) —present, markedly reduced, or absent (3)
19. Fore-tibia of female, inner margin	—large denticles present	—small denticles present
20. Female abdominal sternum VIII, length of basal arm	—long	—short
21. Female abdominal sternum VIII, shape of lateral arms	—arcuate	—more or less straight, divergent
22. Male, aedeagus, internal sac, lobe E	—present	—absent

Table IV. Character states in *Cleonidius* species and related taxa

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
C. erysimi	1	1	1	1	1	2	2	1	1	1	2	1	3	1	1	1	3	2	2	2	2	1
C. eustictorrhinus	1	1	1	1	2	2	1	1	1	1	2	1	3	1	1	1	2	2	2	2	2	1
C. pleuralis	1	1	1	3	1	2	1	1	1	1	2	2	1	1	1	1	2	1	2	2	2	1
C. subcylindricus	1	1	1	1	1	2	2	1	2	2	2	1	2	1	2	1	1	1	2	2	2	2
C. longinasus	1	-1	1	1	1	2	2	1	2	2	2	2	1	1	1	1	3	1	2	2	2	2
C. texanus	1	1	1	1	1	2	2	1	2	2	2	2	1	1	1	1	3	1	2	2	2	2
C. americanus	2	2	2	1	2/3	2	2	1	1	1	2	2	2	1	1	1	3	2	2	2	1	1
C. frontalis	2	1	2	1	2/3	2	1	1	1	1	2	1	2	1	1	1	3	2	1	2	2	1
C. canescens	1	2	1	1	2/3	2	1	1	1	1	2	1	3	2	1	1	2	2	2	1	1	1
C. infrequens	1	3	1	1	2	2	2	1/	1	1	2	1	2	1	1	1	2	3	1	2	1	1
C. puberulus	1	3	1	1	3	2	2	1	1	1	2	1	2	2	1	2	2	2	2	1	1	1
C. collaris	1	1	1	1	2	2	1	1	1	1	2	1	2	2	1	2	2	1	2	1	1	1
C. notolomus	1	1	1	1	2	2	1	1	1	1	2	1	2	2	1	2	2	1	2	2	1	1
C. poricollis	1	1	1	1/2	2	2	2	1	1	1	2	1	3	1	1	1	3	1	2	2	1	1
C. calandroides	1	1	1	1/2	2	2	1	1	1	1	2	1	3	1	1	1	2	1	2	2	1	1
C. boucardi	1	1	1	1	2	2	2	2	2	1	1	1	1	1	2	1	1	1	1/2	2	1	1
C. trivittatus	1	1	1	1	2	2	1	2	1	1	1	1	3	1	2/3	1	2	2	1/2	2	1	1
C. placidus	1	1	1	1	1	2	2	2	1	1	1	1	3	1	2/3	1	3	2	2	1	1	1
C. quadrilineatus	1	1	1	1	2	2	1	2	1	1	2	1	3	1	3	1	3	2	2	2	1	1
C. vibex	1	2	1	1	2	2	1	1	1	1	2	1	3	2	1	1	1	3	2	1	2	1
Lixoglyptus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Cylindropterus	1	1	1	1	/	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Phylogenetic relationships of included species

Distribution of character states is shown in Table IV.

In contrast to *Apleurus*, confidence in phylogenetic relationships in *Cleonidius* is low, due to the low numbers of primary characters as compared to the number of species in the genus, but especially the level at which the primary characters are applicable. Seven of the ten primary characters apply to lineages of only 2 or 3 species; only 3 apply at more general levels, one of which is used to define the monophyly of *Cleonidius* (Fig. 236). This leaves a large number of relationships subject to resolution only on the basis of secondary characters (Fig. 237). Unfortunately, secondary characters containing any phylogenetic information are also not numerous, few are applicable at a general level, and many, especially the latter, are subject to marked homoplasy within *Cleonidius* (Fig. 237).

Basal relationships among *Cleonidius*, *Cylindropterus* and *Lixoglyptus* are very unclear and, as discussed elsewhere (see "Phylogenetic relationships of genera of New World Cleonini") are left as unresolved (Fig. 237). Monophyly of *Cleonidius* however, is strongly supported by the presence of a variously internally (dorsally) developed glabrous shiny median tubercle at the base of abdominal sternum VII of the female. All secondary characters used in support of monophyly of *Cleonidius* involve homoplasy within *Cleonidius* (Fig. 237).

Relationships of the Palearctic species component of *Cleonidius* are herein left as unresolved because of unavailability of series of specimens of *C. vibex* and lack of specimens of other Palearctic species that are potentially *Cleonidius*. Further examination of Palearctic taxa should resolve the placement of the Palearctic species component of *Cleonidius*.

Among species groups, monophyly of each of the *C. boucardi* and *C. poricollis* groups is substantiated by a single primary character (Fig. 236) and also in the *C. boucardi* group by an additional two secondary characters (Fig. 237). Other species groups are defined as monophyletic strictly on the basis of secondary characters, some of which involve extensive homoplasy. Monophyly of the *C. poricollis* group, which contains only two species, is based upon the primary character of presence or absence of a curved sulcus behind the eye. The apotypic state is found in both *C. poricollis* and *C. calandroides*, but, not in all individuals of either species. Monophyly of the *C. boucardi* group is based upon the emarginate or sinuate apex of the dorsal median pocket of the internal sac of males, larger size (secondarily reduced in *C. quadrilineatus*), and reduced pronotal postocular lobes (homoplasious in *C. canescens*). In the *C. americanus* group, monophyly is based upon the ventral tarsal pilose pads being reduced in extent (homoplasious in other *Cleonidius* and other Cleoninae). High incidence of brachyptery and of a mottled elytral scale pattern may further support monophyly of this group. Monophyly of the *C. erysimi* group is based upon apotypic states of two secondary characters of abdominal sternum VIII of female; lateral arms straight; and basal arm short. Both of these characters exhibit homoplasy elsewhere in *Cleonidius*.

Within the *C. erysimi* group, three primary characters indicate that *C. subcylindricus-C. texanus-C. longinasus* comprise a monophyletic group. Relationships of this lineage to the rest of the species group, however, are unclear (Fig. 237). *Cleonidius erysimi* and *C. eustictorrhinus* are considered sister-species, and this lineage along with *C. pleuralis* and the *C. subcylindricus-C. texanus-C. longinasus* lineage, are left as elements of an unresolved trichotomy. *Cleonidius texanus* and *C. longinasus* are regarded as sister-species because they lack large punctures apically on the rostrum and have long dorsal erect vestiture. *Cleonidius subcylindricus* is therefore sister to the *C. texanus-C. longinasus* lineage.

In the *C. americanus* group, primary characters support only the sister-species status of each of *C. americanus* and *C. frontalis*, and *C. infrequens* and *C. puberulus* (Fig. 236); all other relationships are based on secondary characters (Fig. 237). *Cleonidius notolomus* and *C. collaris* are regarded as sister-species based upon pronotal sculpture although the state in *C. collaris* is much more extreme in its irregularity than that in *C. notolomus*. A moderately broad rostrum is used to propose monophyly of the *C. canescens-C. infrequens-C. puberulus-C. notolomus-C. collaris* lineage, and sharp lateral margins of the rostrum, the sister group status of the *C. infrequens-C. puberulus* and *C. notolomus-C. collaris* lineages. Acceptance of the *C. notolomus-C. collaris* lineage as having a secondarily plesiotypic, more elongate-narrow rostrum and of *C. puberulus* having secondarily rounded lateral rostral margins is necessitated by the sister-species status of *C. puberulus* and *C. infrequens*. Other interpretations require that these two not be sister-species and are in my view less parsimonious than that presented above. *Cleonidius canescens* is thus the sister-species of the *C. infrequens-C. puberulus-C. notolomus-C. collaris* lineage and the *C. americanus-C. frontalis* lineage sister to the remainder of species in the *C. americanus* group.

In the *C. boucardi* group, *C. boucardi* is considered sister to the remaining three species in the group based upon the ventral tarsal pilose pads being reduced in extent and the pronotal postocular lobes also reduced (both homoplasious in *Cleonidius*) in the latter three species. *C. quadrilineatus* and *C. placidus* are considered sister-species, with *C. trivittatus* as sister to that lineage, because of long dorsal erect vestiture in the former two species.

In the reconstructed phylogeny of *Cleonidius*, great emphasis is placed on scale pattern because this is the only primary character applicable in a broad or general sense within this genus (Fig. 236). As a result, misinterpretation of distributions of states of other characters are influenced by the topology established on the basis of this one character. If this character is misinterpreted, radical changes in the reconstructed phylogeny would result.

Alternative hypotheses

Alternative hypotheses of phylogeny in *Cleonidius* mainly concern phylogenetic relationships of the species in the *C. boucardi* group. In all other species groups, hypothesized phylogenetic relationships are largely consistent with specific instances of character state intergradation between geographically approximate species (*i.e.,* instances of intergradation are between geographically approximate sister-species) and with geographical distribution of lineages in general (*i.e.,* sister lineages are largely geographically approximate). In the *C. boucardi* group however, this is not so because character state intergradation is marked between each of *C. boucardi*, *C. trivittatus*, and *C. placidus*, none of which are hypothesized as sister-species of any one of the others (see Fig. 237). To be consistent with patterns of intergradation, *C. quadrilineatus* would have to be the sister-species of a lineage composed of *C. boucardi*, *C. trivittatus*, and *C. placidus*, an unfavourable revision in the hypothesized phylogeny that would require additional and unsatisfying homoplasy in the characters of form of the anterolateral margins of the pronotum, and extent of ventral pilose tarsal vestiture, and, reconsideration of long suberect or erect body vestiture as plesiotypic for the species group. Ability to interbreed, presumably the likely cause of the intergradation, is a plesiotypic feature and thus cannot be used as evidence of common ancestry although it may be tempting to do so.

Alternatively, the observed intergradation in character states among *C. boucardi*, *C. trivittatus*, and *C. placidus*, geographically approximate distributions of the three, and association with Leguminosae for at least *C. trivittatus* and *C. placidus* (plant relationships are

unknown in *C. boucardi*), could warrant recognition of only a single species composed of three geographically distinct forms.

I do not favour either of these approaches, the former because it necessitates additional homoplasy, and the latter because it necessitates extensive polymorphism in a number of otherwise phylogenetically informative characters. I prefer recognition of three species, and attribute the geographical inconsistency to the host shift from Leguminosae to Roseaceae/Rhamnaceae in *C. quadrilineatus*, which has likely promoted structural differentiation in that species and which has permitted redispersal such that *C. quadrilineatus* is now largely sympatric with other members of the *C. boucardi* group.

EVOLUTIONARY ANALYSIS: BIOGEOGRAPHY
Methods of Biogeographic Analysis

Historical and ecological factors combine to produce the observed distributions of plants and animals, the explanation of which is the goal of the science of biogeography. Unfortunately many past studies of biogeography attempt to explain the distributions observed in terms of only one of ecology or history (Endler, 1982). Distinguishing the relative roles of these factors must at least be considered although most agree it is very difficult to separate the effects of the two and to estimate their relative roles (Endler, 1982; Vuilleumier and Simberloff, 1980). The present study is no exception and my approach, although attempting to encompass aspects of both historical and ecological biogeography, will be largely historical in its focus.

Knowledge of distribution and aspects of natural history combine with knowledge of phylogenetic relationships and of earth history to allow for discussion of the historical biogeography and ultimately, the evolutionary history of the taxon in question. Ecological biogeography on the other hand does not require knowledge of phylogeny and earth history, but rather ecological theory and principles. Systematists and ecologists are the proponents of the historical and ecological approaches respectively. Rarely are the two approaches combined in a single study and relative roles assessed. This is brought about simply by the nature of the data bases because systematists frequently have not carried out the detailed sampling necessary for the application of ecological theory. Similarly, more often than not, ecologists do not have the knowledge of phylogeny that predicates all historical biogeographic analyses.

In ecological biogeography, the units selected for study are usually communities or various guilds of taxa that share association with a particular resource, be it habitat, food, geographic area, *etc.* (Cody and Diamond, 1975). Ecological biogeographers are primarily concerned with temporally proximate factors that determine the composition of the species assemblage but not the origins of these same factors. Little concern or attention is expressed or given to the phylogenetic relationships of the constituent taxa and thus there is a large or even total disregard for historical components because notions about the latter can only be developed in terms of detailed knowledge of phylogeny. Less frequently, ecological determinants of distributions of constituents of monophyletic groups, say a genus or family, have been studied, although rarely if at all with specific reference to detailed phylogenetic relationships.

Much of ecological biogeography addresses questions of dynamics and proximal origins of diversity, best applicable to islands or insular situations. Diversity patterns on continents are much more complex and are not so easily studied. Unfortunately, knowledge of population dynamics and detailed data about natural history attributes, permitting determination of niche breadths, are required for much meaningful ecological biogeography to be conducted (Cody, 1975; Pianka, 1975). Because of this, the approach I will take herein is only one of examination

of natural history attributes and distributions, with specific reference to present environmental parameters.

Historical biogeographers, on the other hand, recognize and stress the need for knowledge of phylogeny, but generally at the expense of ignoring the role ecology might play in determining distributions. Indeed, to many, knowledge of phylogeny is essential prior to attempts at any meaningful historical biogeography. Wiley (1981) has noted three schools of historical biogeographers: 1, evolutionary; 2, phylogenetic; 3, vicariance (or panbiogeographic, although Croizat [1982] has disputed this). Detailed knowledge of phylogeny and strictly monophyletic groups are the units of study for adherents of phylogenetic and vicariance biogeography and stress vicariance and allopatric speciation. Evolutionary biogeography however, emphasizes the role of dispersal with little or no regard for speciation mechanism or for details of phylogeny. This latter is not employed by many contemporary biogeographers for it is the approach resulting in the narratives and "scenarios" frowned upon for their *ad hoc* nature, and lack of applicability and rigour. Heuristic advantages of the phylogenetic and vicariance schools of biogeography are consistent with the advantages of a phylogenetic approach to phylogeny reconstruction and are discussed in more detail by Wiley (1981), Patterson (1981), and Platnick and Nelson (1978).

Ball (1975) recognizes three phases through which biogeographic studies pass: 1, descriptive or empirical phase; 2, narrative phase; and 3, analytical phase. These phases, as noted elsewhere herein and by Patterson (1981), apply equally well to systematic studies, especially methods of phylogeny reconstruction. Descriptive or empirical biogeography is simply the data base. What are the extant distributions and natural history attributes of the taxa in question? What habitats do they occupy? What do they eat? When are they active?

In large part, narrative and analytical phases contrast inductive and hypothetico-deductive approaches to biogeographic studies. Narrative explanations, or general evolutionary "scenarios" as they have been called by Eldredge (1979), have frequently been criticized as pseudo-science or bad science because of their unfalsifiable and *ad hoc* nature, and for their explanatory value, which is, more often than not, concerned only with particulars as they apply to the taxon in question (Goudge, 1961; Hull, 1974; Ball, 1975; Eldredge, 1979; Eldredge and Cracraft, 1980; Brown and Gibson, 1983). General applicability is not usually a concern of narrative explanations, although there is no reason why it should not be.

Consequently, Eldredge (1979) notes two ways of improving these "scenarios". Firstly, base them more explicitly on knowledge of phylogenetic relationships, and secondly, eliminate some if not all of the more purely speculative elements. To these suggestions, I add a third; formulate explanations as hypotheses in terms that are testable, predictive, and have potential for more general applicability than just the taxon in question. With these improvements in mind, "scenarios" are capable of producing ideas that can be subsequently rigorously tested in a hypothetico-deductive manner for acceptance as general scientific facts, ideally of widespread applicability and significance. In essence, this is the analytical phase of Ball (1975).

In my analysis of historical biogeography I employ a phylogenetic approach to place aspects of the phylogeny of North American Cleoninae in a geographic perspective and thus come to some degree of understanding of the geographic history of that specific taxon. Resultant potential generalizations and predictions based on these results are enumerated, discussed and formulated as hypotheses of general potential utility.

A vicariance approach, examining distribution patterns of other North American arid land taxa and the plotting of generalized tracks will not be attempted herein but should be carried

out as more studies of such taxa, that include a phylogenetic basis, become available.

Genus *Apleurus* Chevrolat

Diversity patterns

The genus *Apleurus* is represented in arid land habitats of southwestern North America and Mexico by eight species placed in two subgenera. Maximum species diversity is in southern California, northwestern Mexico (including Baja California Norte), southern Arizona and southern New Mexico (Fig. 230). Diversity decreases beyond this area especially to the east and the north. Species of *Apleurus* do not occur north of 45°N latitude, east of 95°W longitude, or south of 15°N latitude (Fig. 230).

Five of the eight species are stenotopic, variously restricted in their distributions and of these five, only two, *A. jacobinus* and *A. hystrix* are macrosympatric. The remaining three species, *A. lutulentus*, *A. angularis*, and *A. albovestitus*, are eurytopic, widespread and broadly sympatric with each other and various of the five geographically restricted species. Gross geographic range overlap is relatively low with 12 of 28 possible species pairs (42.8%) having at least partial sympatry. Nine of the 12 sympatric species pairs exhibit overlapping distributions; three are nested (the area of distribution of one species occurring entirely within the area of distribution of the other).

Habitat associations

Habitat associations of the species are varied, ranging from grasslands to desert-grassland transitional habitats or deserts in eurytopic species (three of the eight); others are more stenotopic, found only in grasslands, desert-grassland transitional habitats, or in deserts (five of the eight) (Fig. 238).

Apleurus aztecus is a mesquite-grassland inhabitant in central México. *Apleurus lutulentus*, although also found in desert-grassland transitional habitats, is primarily a mesquite-grassland and grassland inhabitant as evidenced by its more easterly distribution into eastern Texas, Oklahoma and Kansas and disjunct southerly distribution into central México, but not in the Mexican portion of the Chihuahuan desert (Fig. 207). *Apleurus angularis* is also found in grasslands, however, in contrast to *A. lutulentus*, does not extend as far east or south as does that species. Rather, *A. angularis* extends further west and north into Great Basin desert. *Apleurus jacobinus* and *A. porosus* are semi-desert and semi-desert to desert inhabiting species respectively. *Apleurus albovestitus* is distributed even more to the west than is *A. angularis*. It occurs in most western semi-desert and desert, and desert-grassland transitional habitats. *Apleurus saginatus* is a desert-grassland inhabitant bordering the eastern Sonoran Desert region (Fig. 206). *Apleurus hystrix* is a sand dune inhabiting species in the California semi-desert habitat.

Relative measures of association of species with particular types of habitats reveals a slightly higher level of association with desert-grassland transitional habitats than with others. These measures were obtained by summing the total number of species of *Apleurus* occupying a particular habitat type scoring one for a marked association (solid box in Fig. 238) and one-half for a less marked association (half box in Fig. 238). This number is then divided by the number of possible associations with that habitat type to give a relative measure of the degree to which species of the genus occur in the various habitat types. Measures of association with the four desert habitats is 0.156; with semi-deserts, 0.250; with desert-grassland transition

habitat, 0.375; and, with mesquite-grasslands and grasslands, 0.313.

Plant associations

Details of host plant associations are largely unknown for all species and so all plant associations, many likely accidental, have been used as indicative of the probable taxonomic range of host plants (Fig. 239). Adults of all species are found primarily or exclusively on Compositae although in some species, especially *A. albovestitus*, adults are found sporadically on a variety of other types of plants as well. Other than Compositae, Chenopodiaceae and Leguminosae constitute the bulk of the remainder of the associations. Clear associations with taxa lower than the hierarchical level of family are not evident.

Altitudinal zonation

Altitudinal ranges are shown as a Hubbs-Hubbs diagram (Fig. 232). Although species may be represented over an extensive range of altitudes, most members of each species are found over a narrower part of this range.

Apleurus hystrix, *A. jacobinus* and *A. porosus*, species restricted to the Pacific coastal areas, are found over a much narrower range of altitudes than are more widespread species. Altitudinal ranges of these three coastal species overlap extensively. On the other hand, among the remaining species, only *A. lutulentus* and *A. aztecus* have altitudinal ranges which overlap extensively. The three remaining species, *A. angularis*, *A. albovestitus*, and *A. saginatus*, have altitudinal ranges which differ from each other, and from any other species in the genus. There is, in general, little overlap in the altitudinal ranges of species of *Apleurus* (Fig. 232). There is also a trend towards occupation of lower altitudes by increasingly derived species in the genus.

Seasonal occurrence

Patterns of adult seasonal occurrence are broad with *A. angularis*, *A. jacobinus*, *A. albovestitus* and *A. saginatus* found throughout the year. *Apleurus porosus* adults are found from January to November and are likely active throughout entire year. On the other hand, *A. lutulentus* adults are known from March to October; *A. aztecus* from June to August; and *A. hystrix* from February to July. Few records are available, however, for these last two species. Detailed life histories are unknown for all species.

Co-existence

Consideration of these various niche dimensions as a group reveals that no two species of *Apleurus* share the same or largely overlapping ranges in all niche dimensions. Statistical measures aside, inspection shows species differences along the dimensions of altitude, geographic distribution, and habitat association. All species share a plant association with Compositae. Macrosympatric species differ in various aspects of altitudinal range and habitat association. Species with overlapping altitude ranges are allopatric or differ in habitat association. In general, niche overlap between species of *Apleurus* is low.

Wing length polymorphism

At least some adult members of most *Apleurus* species lack wings; 97.9% of *A. lutulentus*, 4.5% of *A. angularis*, 99.8% of *A. albovestitus*, and all *A. saginatus* are the only macropterous individuals known. Adults examined of species of restricted distribution such as *A. hystrix*, *A. aztecus*, *A. jacobinus* and *A. porosus* are all apterous. The most widespread species, *A.*

albovestitus, *A. lutulentus* and *A. angularis* have various percentages of macropterous individuals. These individuals are scattered throughout the species ranges and are not restricted in their distributions.

<div align="center">Genus Cleonidius Chevrolat</div>

Diversity patterns

The genus *Cleonidius* is represented in North and Central America by 19 species; a single species has so far been recognized from the Palearctic Region but is not considered further in the biogeographic discussions following. Maximum species diversity is in the southwestern United States, especially southern and central California, southern Nevada, Arizona, southern Utah, New Mexico, Colorado and western Texas (Fig. 231). Diversity decreases slightly to the north in northern Utah and Wyoming into eastern Washington and western Montana, but more markedly into Oregon and western Washington to the west, into eastern Texas, Oklahoma and Kansas to the east, and especially to the south into México (Fig. 231) (although this may prove an artifact of insufficient collecting). Species of the genus extend north into southern Canada and south as far as Honduras; two species occur along the east coast of North America.

Species of *Cleonidius* tend to be more or less widespread in their geographic distributions. I consider only five of the nineteen species restricted in their geographic distributions. Three of these five, *C. americanus*, *C. placidus*, and *C. eustictorrhinus* are macrosympatric and found only in California; *C. collaris* is found only in eastern Colorado and nearby localities in adjacent states; and *C. calandroides* is found only along the northern Atlantic coast. Three other species (*C. puberulus*, *C. notolomus*, and *C. infrequens*) are slightly less restricted in their distributions. Of the remaining 11 species, 10 are moderately to very widespread in the western or southwestern United States and Mexico and are largely macrosympatric with each other and with various of the species with restricted distributions. One species, *C. subcylindricus*, is found along the Atlantic Coastal Plain. One of the six species in the *C. erysimi* group, one of two in the *C. poricollis* group, one of four in the *C. boucardi* group, and five of seven in the *C. americanus* group have more or less restricted distributions.

Gross geographic range overlap is slightly more extensive than in *Apleurus*. In the *C. erysimi* group, eight of 15 possible species pairs have at least partial sympatry (three overlapping, five nested); two of six comparisons in the *C. boucardi* group (two overlapping) and 11 of 21 in the *C. americanus* group (seven overlapping, four nested) result in at least partial sympatry. Species in the *C. poricollis* group are allopatric. For the genus *Cleonidius* as a whole, 87 of 171 possible combinations result in at least some sympatry (62 overlapping, 25 nested). In other words, a single species is on average macrosympatric with 50.9% of the genus, or 9.67 other species of *Cleonidius*.

Habitat associations

Habitat associations are varied in species of the genus, ranging, as in *Apleurus* species, from grasslands to deserts in some, to principally deserts, to principally grasslands in others (Fig. 240). Measures of primary habitat associations (calculated as for *Apleurus* species), differ slightly from those in *Apleurus* however, because in *Cleonidius*, association with desert habitats is low (0.099), increasing in semi-desert habitats to 0.171, and desert-grassland transitional habitats to 0.316. The highest association is with mesquite-grasslands and grasslands (0.474). Association with western xerophytic evergreen forest is 0.132 whereas no

Apleurus were associated with this habitat type. Among the species groups, the *C. erysimi* group is relatively well represented in deserts (0.125), also in semi-desert (0.250), but less so in desert-grassland (0.167) and markedly less so in mesquite-grasslands and grasslands (0.083). In contrast, the *C. americanus* group has values of 0.054 for deserts, 0.107 for semi-desert, 0.429 for desert-grassland, and 0.714 for mesquite-grasslands and grasslands. The *C. boucardi* group has values of 0.000, 0.125, 0.250, and 0.500 respectively for these same habitats. The only southwestern species in the *C. poricollis* group is found in a variety of habitats. With the exception of this species, *C. poricollis*, other *Cleonidius* species are restricted to one or only a few habitat types.

Plant associations

Unlike in *Apleurus* species, which are all associated primarily with Compositae, plant associations in *Cleonidius* species are much more varied and span a much broader taxonomic range of plant families (Fig. 241). A number of species are associated with Compositae, Rosaceae, Cruciferae, and Leguminosae. There is slight association with Chenopodiaceae and scattered records of associations with members of various other plant families. In the *C. erysimi* group, associations are varied, with one species on each of Compositae, Rosaceae and Rhamnaceae, and Cruciferae, and two on Leguminosae. Plant associations are not well known for *C. eustictorrhinus*. In the *C. boucardi* group, two species are associated with Leguminosae, one species with Rosaceae and Rhamnaceae, but also Leguminosae; plant associations are not known for *C. boucardi*. Associations are primarily with Compositae and Cruciferae in *C. poricollis*; exclusively with Cruciferae in *C. calandroides*. Finally, plant associations are few for most species in the *C. americanus* group with the exception of *C. americanus* which appears to be associated with Compositae.

Altitudinal zonation

Altitudinal ranges are shown as a Hubbs-Hubbs diagram (Fig. 233). In general, each species is found over a wide range of altitudes which overlap extensively with ranges of many other species such that *Cleonidius* species are not as markedly altitudinally segregated as are *Apleurus* species. This marked overlap also exists within each of the species groups as well. *Cleonidius poricollis*, and three members of the *C. boucardi* group, *C. boucardi*, *C. trivittatus* and *C. quadrilineatus*, have the largest altitudinal ranges of species in *Cleonidius*. Individuals of these species have been recorded at maximum altitudes ranging from 3276 to 4004 m.

Seasonal occurrence

Patterns of adult seasonal occurrence are broad with most species found throughout the greater part of the year from early spring to late winter months.

Co-existence

In contrast to species of *Apleurus*, examination by inspection of niche dimensions as a group shows the majority of *Cleonidius* species differ most in terms of host plant (Fig. 241) and habitat associations (Fig. 240). Species geographic range overlap is generally high (see Table V), as is the degree of altitudinal range overlap and as is overlap in seasonal occurrence. Within the *C. erysimi* group, extent of sympatry and altitudinal range overlap are high, but different species in the group are associated with different habitat types and with different plant families. In the *C. americanus* group, extent of sympatry and altitudinal range overlap are low

Table V. Chorological relationships of *Cleonidius* species

	C. erysimi	*C. eustictorrhinus*	*C. pleuralis*	*C. subcylindricus*	*C. longinasus*	*C. texanus*	*C. americanus*	*C. frontalis*	*C. canescens*	*C. infrequens*	*C. puberulus*	*C. collaris*	*C. notolomus*	*C. poricollis*	*C. calandroides*	*C. boucardi*	*C. trivittatus*	*C. placidus*
C. eustictorrhinus	S																	
C. pleuralis	BS	A																
C. subcylindricus	A	A	A															
C. longinasus	BS	S	A	A														
C. texanus	BS	S	BS	A	BS													
C. americanus	S	S	P	A	S	S												
C. frontalis	BS	P	BS	A	BS	BS	S											
C. canescens	BS	A	BS	A	A	NS	BS	P										
C. infrequens	P	A	A	A	A	S	A	A	A									
C. puberulus	S	A	A	A	A	S	S	A	S	S								
C. collaris	S	A	A	A	A	S	S	A	S	S	A							
C. notolomus	P	A	S	A	S	A	S	S	NS	NS	A	A						
C. poricollis	BS	A	BS	A	BS	BS	S	S	S	S	S	S	A					
C. calandroides	A	A	A	NS	A	A	A	A	A	A	A	A	A	A				
C. boucardi	P	A	P	A	A	NS	NS	A	A	A	A	A	P	A	A			
C. trivittatus	BS	P	BS	A	BS	BS	BS	P	BS	S	BS	S	BS	P	BS	P		
C. placidus	S	S	P	A	S	S	S	S	A	S	A	A	S	A	A	A	P	
C. quadrilineatus	BS	S	A	A	BS	BS	BS	S	BS	S	NS	BS	S	A	S	A	A	BS

S, sympatric ; BS, broadly sympatric ; NS, narrowly sympatric ;
P, parapatric ; A, allopatric.

and habitat associations overlap extensively; plant associations are mostly unknown. In the *C. boucardi* group, sympatry is low, habitat associations differ, host plant associations differ slightly, but altitudinal range overlap is high.

The genus *Cleonidius* is more diverse than *Apleurus* and is more extensive in its distribution. Whereas *Apleurus* species appear to be more associated with deserts and less so with grasslands, *Cleonidius* is very well-diversified in grasslands and desert-grassland transitional habitats and is not associated with deserts to any significant degree (except for species in the *C. erysimi* group). Only in *Cleonidius* are some species associated with the western xerophytic evergreen forest. Patterns in host plant association differ markedly, for species of *Apleurus* are almost exclusively associated with Compositae, whereas species of *Cleonidius* are associated to various degrees with one of Compositae, Cruciferae, Leguminosae, Rhamnaceae, Rosaceae and to a lesser extent Chenopodiaceae.

Wing length polymorphism.— All individuals examined of the *C. boucardi* group are macropterous; in the *C. poricollis* group 99% of *C. poricollis* and all *C. calandroides* are macropterous; and, in the *C. erysimi* group, only in *C. erysimi* are brachypterous individuals known (91%). In contrast, in the *C. americanus* group, all *C. canescens*, *C. puberulus* and *C. collaris*, and 79% of *C. notolomus* and 38% of *C. infrequens*, are brachypterous.

Apleurus and *Cleonidius*: Historical biogeography of New World species

Introductory Comments – A Warning

The evolutionary history of plant and animal taxa that presently inhabit the southwestern United States and adjacent areas has been very complex. Not surprisingly, determination of what this history has been is also a very difficult task and based on various assumptions. Changing, locally variable climates, mainly a trend during the Tertiary of increasing aridity (but here and there punctuated by pluvial periods of various duration) resulting in various and ephemeral habitat types, continual but localized orogenic activity, and locally variable topography, all result in a complex framework for speciation events to be understood and even approximately dated. Adding to this is perhaps the most significant problem, that of the Quaternary, for it is known that distributions of many organisms changed radically during this time period (Coope, 1979). Owing to these presumptive changes, many of the distribution patterns may reflect only Quaternary distributional shifts and not original speciation events, these perhaps having occurred elsewhere and under very different ecological conditions. In other words, the present distributions may be the result of secondary, not primary contact zones (Endler, 1977). In the absence of fossils, the heuristic value of historical biogeography may therefore be questioned because in order to overcome this problem, assumptions about habitat associations, other ecological attributes, and especially distributions of the species at different times, or of their ancestors, are required, based on these features in extant species. These can only be made with reference to a reconstructed phylogeny and as such the claim of phylogeny before biogeography is in large part valid for analyses to be maximally scientific. Whether or not these assumptions should be accepted is a moot point.

Because biogeographic statements are so dependent on a reconstructed phylogeny, another problem is that of confidence in the reconstructed phylogeny. A weak reconstructed phylogeny results in weak biogeographic statements that may prove misleading should they be uncritically accepted as facts.

In *Apleurus*, only the possibility of changed distributions is a problem, for confidence in the reconstructed phylogeny is high. On the other hand, both are problems in *Cleonidius*. Confidence in the fully resolved reconstructed phylogeny is low due to the large number of secondary characters used in the analysis and concomitant homoplasy in these characters. Some biogeographic statements about details of species origins in *Cleonidius* must therefore be cautiously accepted, and alternatives, some of which are discussed, must also be considered.

A further complication in *Cleonidius* is recognition of a Palearctic species component which is not herein considered in the reconstructed phylogeny. The single species examined from the Palearctic region can, however, be placed either as sister to the Nearctic *Cleonidius*, or as a member of the *C. americanus* group. Biogeographic significance of both placements will be discussed.

Historical Explanations

In *Apleurus*, diversity gradients do not appear to be easily explainable in terms of latitude, elevation, or any other climatic factor with the possible exception of regional degree of variation in aridity. As noted elsewhere, evolution of *Apleurus* appears to parallel evolution of increasingly arid habitats. This is supported by comparison not only of habitat associations with the reconstructed phylogeny (Fig. 238), but also of altitudinal ranges with the reconstructed phylogeny which trend toward occupation of lower, and thus likely more arid altitudes. Thus, if any ecological factor might prove important in explaining why southern California, Arizona, New Mexico and extreme northwestern Méhave the highest species diversity (Fig. 230), it is likely the degree of habitat and associated floral complexity largely due to the occurrence of desert and desert-grassland transitional habitats in these areas. Species diversity drops markedly beyond the area where these habitats occur.

Similarly, in *Cleonidius*, maximum species diversity is again noted in these same areas, but is also high throughout the rest of Arizona and New Mexico, western Texas, central California, and southern Nevada, Utah, Colorado and Wyoming (Fig. 231). Species diversity thus appears again to be influenced by degree of arid habitat complexity. However, high species diversity is more widespread in *Cleonidius* because of the higher level of association of the species in the genus with more widespread grassland and woodland habitats (Fig. 240). Although evolution in this genus has likely also been influenced by increasing aridity in southwestern North America, these influences are not as clearly indicated as in *Apleurus*. In *Cleonidius*, adaptation to the most arid habitats is low, and to the least arid, relatively high. Furthermore, there is no clearly evident evolutionary trend for species of the genus to be found in increasingly arid habitats (Fig. 240), or at successively lower altitudes as are noted in *Apleurus*. High diversity in *Cleonidius* thus extends outside the area of the highest habitat complexity and especially into areas of grassland, woodland, and desert-grassland transitional habitats. High degree of association with less arid habitats also explains the broader geographic and altitudinal range of the species in the genus and perhaps also the occurrence of the genus in the Palearctic region as well. In addition to the effects of habitat on the evolution of the group, unlike *Apleurus*, which are all apparently associated with Compositae, species of *Cleonidius* are associated with a much broader taxonomic array of plants (Fig. 241). Clearly, host plant shifts are an additional factor to consider in the evolution of this latter genus.

In the present study I address the hypothesis that evolution and speciation within *Apleurus* and *Cleonidius* closely parallel increasing aridity and associated changes in distribution and composition of habitat types in the southwestern United States and Mexico. History of

distribution and composition of habitats in these areas has been dealt with extensively in paleobotanical studies by Axelrod (1950, 1975, 1979, 1985), Axelrod and Raven (1985) and Raven and Axelrod (1978) and thus interpretation of the geographical history of *Apleurus* and *Cleonidius* draws largely upon the results of these publications.

Of three possible origins of arid land faunas in North America, only two are likely for Cleonini. First, as discussed by Axelrod (1975), a continuous North American-western Eurasian belt of Madrean-Tethyan sclerophyll woodland vegetation may have lived in the early Paleogene, with subsequent vicariance of this habitat, as a result of Atlantic Ocean floor spreading, proposed to account for any present disjunctions in distributions. Secondly, and perhaps the generally more favourable hypothesis, Webb (1977) notes the marked similarity between savanna-adapted mammal faunas in Asia and North America in the late Eocene (postdating similarities between the faunas of Europe and North America), and invokes subsequent vicariance of these habitats across Beringia as responsible for present distributions. A third possibility, South American origins, as noted by Raven (1963) and Wells and Hunziker (1976) for various plants, does not appear likely, because no Cleonini are known from that continent (Wibmer and O'Brien, 1986) and the *Lixus* known from there do not appear related to *Cleonidius*.

Apleurus seems to be North American in origin and likely evolved *in situ*, on Compositae, in isolation from its sister genus, the Palearctic *Chromoderus*, as a result of vicariance of sclerophyll woodland or savanna habitats in Holarctica, either between western Europe and North America no later than early Eocene or between eastern Asia and North America no earlier than the late Eocene (Fig. 242) respectively. Accepting that *Apleurus* evolved in North America and on Compositae, investigation of the role of history proceeds by examination of distributions and aspects of natural history with respect to the reconstructed phylogeny.

First, aside from *A. hystrix*, the next two most plesiotypic species, *A. aztecus* and *A. lutulentus*, are exclusively and primarily mesquite-grassland and grassland inhabiting species, respectively (Fig. 238). This, and the increased association of more derived species with semi-desert and desert habitats, demonstrates a clear trend from mesquite-grassland and grassland to desert habitation within species of the genus (Fig. 238), and indicates that mesquite-grasslands, grassland, or a precursory habitat type not present today, or present but lacking association with any *Apleurus* species, was likely the ancestral habitat for the genus. This habitat was likely a grassland or savanna habitat, because no *Apleurus* are known from woodland habitats, plesiotypic *Apleurus* are currently associated with this or a similar type of habitat (Fig. 238), no eastern North American *Apleurus* are known, and *Chromoderus* species judging from their distributions, are likely steppe or grassland inhabitants. In view of this, a trans-Beringian savanna or grassland vicariance origin of *Apleurus* (Fig. 242) is to be preferred over the Madrean-Tethyan vicariance of Axelrod (1975), which would predict southwestern North America-Mediterreanean area relationships, presence of plesiotypic species in woodland habitats, presence of plesiotypic species in southeastern North America, and presence of closely related taxa in similar extralimital woodland habitats.

Grasses were present in North America in the early Tertiary as evidenced by first appearance of grass pollen in the Paleocene, and first grass macrofossils and first appearance of structural adaptations in mammals to open habitats (including especially, the initial albeit slight development of high crowned teeth resistant to the abrasive properties of grasses) in the Oligocene (Clayton, 1981; Webb, 1977).

Savanna or woodland precursors of mesquite-grassland and grassland and desert habitats likely first emerged as distinct habitats in the mid- to late-Eocene as a result of a slowly expanding dry climate and a marked increase in seasonal aridity fostering *in situ* adaptation by already existing subhumid plants to these new and increasingly semi-arid conditions (Axelrod, 1950, 1975, 1979; Axelrod and Raven, 1985; Cronquist, 1978; Webb, 1977). Arboreal vertebrates are less frequent in fossil deposits of this age, a number of North American groups developed special adaptations to savanna habitation, and new, savanna-adapted groups emigrated from Asia where they had already developed their adaptations for this type of life (Webb, 1977). Adaptation and radiation in animals and plants (especially dicotyledonous herbs) continued into the Oligocene as arid habitats proceeded to expand and diversify (Axelrod, 1979; Cronquist, 1978; Webb, 1977). At this time semi-arid woodland or savanna habitats were apparently relatively extensive in North America (Axelrod, 1975) and were likely interspersed with localized grasslands. Both faunas of late Eocene (Webb, 1977), and floras of the Oligocene (Axelrod, 1979), document relationships between taxa in southern California and those in the Rocky Mountain region (Axelrod, 1975; Raven and Axelrod, 1978). Axelrod (1979, Figure 6) and Raven and Axelrod (1978) further note that a number of congeneric "closely related" woodland taxa are presently disjunct in insular and maritime southern California and the highlands of central México. A continuum may therefore have commented these two areas and perhaps also the southern Rocky Mountain region from perhaps the late Eocene, at the earliest, into the Miocene (Axelrod, 1950; Raven and Axelrod, 1978). The present woodland in the uplands of central México is the habitat thought to be most like the ancestral Oligocene-Miocene woodland, hence the name Madrean for this vegetation type (Axelrod, 1975, 1979). Development of increasingly arid habitats intermediate between these areas throughout the later Tertiary, likely resulted in at least some of these present disjunctions (Axelrod, 1975).

This geographic pattern applies well to *Apleurus* because the most plesiotypic species of *Apleurus*, *A. hystrix*, is found in sand dunes in southern California, whereas the next two most plesiotypic species, *A. aztecus* and *A. lutulentus*, live respectively, inland in central México, and in central México, Arizona, New Mexico, Texas and adjacent states, (Fig. 242). This pattern, although between a California sand dune species and Mexican or southern Rocky Mountain mesquite-grassland and grassland taxa, is geographically similar to the relict disjunctions noted above for semi-arid woodland plants and is suggestive that the same may also apply to taxa initially adapted to savanna or grasslands. If isolation and the relict nature of *A. hystrix* is a result of an early vicariance of California and inland semi-arid grassland or savanna habitats, we might expect similar phylogenetic and geographic relationships to those in *Apleurus* in other taxa in which a structurally markedly distinct species is restricted to one of the southern California coastal dune habitats. Unfortunately, although endemics are known to occur in many California dune fields (Andrews *et al.*, 1979), phylogenetic and geographic relationships of the endemics have not been studied in detail. Most extensive survey efforts have also concentrated principally on inland dune fields (Andrews *et al.*, 1979; Hardy and Andrews, 1976). Some of these endemics are also not of a relict nature and are likely a product of the later Tertiary climatic changes that fostered the rapid and numerous speciation events thought to have contributed so extensively to the marked levels of endemism in the California flora (Stebbins and Major, 1965; Raven and Axelrod, 1978). Perhaps relicts such as *A. hystrix* in California, are managing to survive in restricted or marginal habitats having changed habitat associations from the grassland or savanna habitat perhaps due to exclusion by newly evolved

competitively superior species, or due to the changing nature and ephemeral status of habitats to which they were initially adapted. Raven and Axelrod (1978) note that among plants, a number of Tertiary relicts have survived in California owing to its sheltered and equable climate.

Grassland habitat only reached its present form and more extensive distribution during the Miocene and early Pliocene (but especially at the Miocene-Pliocene transition) (Axelrod, 1950, 1985; Webb, 1977). Because of this, it is unlikely that divergence between *A. aztecus* and the ancestor of the remainder of *Apleurus* took place before this time. Restriction of *A. aztecus* to mesquite-grasslands, and primary association of *A. lutulentus* with mesquite-grasslands and grasslands, suggests that the ancestor of the subgenus *Apleurus*, like the ancestor of the genus *Apleurus* as noted, was also associated with grassland-like habitats. Present restriction of *A. aztecus* to central México is unlikely to have been a result of competitive exclusion by *A. lutulentus* in the grasslands of the United States, for *A. lutulentus* coexists with *A. aztecus* in central México (Figs. 207, 210). Rather, a late Miocene or early Pliocene north-south vicariance of Plains and Mexican Plateau grasslands as a result of increasing aridity and development of more extensive semi-desert habitats (Webb, 1977) can account for the distribution, with a subsequent dispersal of *A. lutulentus* south through desert-grassland transitional habitat into central Mexican mesquite-grasslands and the Hidalgan Desert region (term of Shreve, 1940; Axelrod, 1979) of a later Pleistocene origin. This later dispersal route may have been through a desert-grassland transitional habitat, not grassland or mesquite-grassland, because of the absence of concomitant dispersal north by *A. aztecus*. Alternatively, lack of dispersal by the latter species may be due to individuals being flightless whereas those of *A. lutulentus* are macropterous and presumably capable of flight. Webb (1977) has drawn attention to the role of central México, noting that Miocene faunules from this area play a focal role in the history of the semi-arid biota of North America. Similarly, Cronquist (1978) notes that the tribe Heliantheae of the Asteraceae (Compositae herein) has its present center of diversity in the arid highlands of central México, suggesting that this area has been important in the evolutionary history of the group.

Increased aridity during the middle Pliocene resulted in increased extent of semi-desert habitats and likely the origin of the ancestor of the remainder of *Apleurus* in western desert-grassland transitional habitats, and *A. lutulentus* in more easterly, primarily grassland, habitats (Fig. 243).

Divergence of the *A. porosus-A. jacobinus-A. angularis* and *A. saginatus-A. albovestitus* lineages is more problematical, for extant species of the two groups, especially *A. angularis* and *A. albovestitus*, do not differ much in their habitat associations or distributions.

In the *A. saginatus-A. albovestitus* lineage, an east-west vicariance of desert-grassland and semi-desert habitats respectively (Axelrod 1979, figure 4) as a result of late Quaternary aridity following the increased precipitation of the late Pliocene and early Pleistocene (Axelrod, 1979) likely resulted in the origin of *A. saginatus* and *A. albovestitus* respectively (Fig. 245). Although *A. albovestitus* is presently a widespread species, examination of intraspecific variation shows the most plesiotypic form to be that from coastal Californian semi-desert (possession of large glabrous abdominal patches, deeper and larger punctation; see "Geographic variation" of *A. albovestitus*). Presence of other forms of *A. albovestitus* to the east in other semi-desert and desert habitats is therefore suggestive of recent dispersal followed by post-glacial local or regional selection pressures in various regional habitats which are hypothesized to be largely of a recent origin in the late Quaternary (Spaulding *et al.*, 1985).

Unlike *A. albovestitus*, *A. saginatus* has not expanded its range and is still found only in the desert-grassland transition bordering the eastern portion of the Sonoran desert (Fig. 206).

In the *A. porosus-A. angularis-A. jacobinus* lineage, patterns of vicariance (Fig. 244) among the three species are clearly evident for they are allopatric (Figs. 208, 210–211). Because it has only been during the last four million years that Baja California reached its present position and acquired a notably drier climate and coastal foggy desert (Axelrod, 1979), origin of *A. porosus* does not likely predate that time. Increased aridity in the area likely allowed entry of a desert-grassland-adapted ancestor from the north, as Baja California was reaching its present position. This form is presumed to have evolved *in situ* into *A. porosus*. An east-west vicariance of desert-grassland and semi-desert-adapted populations of the ancestor of *A. jacobinus-A. angularis*, as in the *A. albovestitus-A. saginatus* lineage, likely accounts for the origin and present distribution of *A. jacobinus* and *A. angularis* . Present distributions of *A. porosus* , *A. jacobinus*, and *A. angularis* may be maintained as allopatric by competitive exclusion or by selection pressures promoting reproductive isolation.

For *Apleurus* then, increasing aridity and concomitant changes in habitat structure and availability appears to be the scenario most consistent with ideas and evidence about paleoenvironments and their distribution in space and time in southwestern North America.

In *Cleonidius*, the pattern is somewhat different. *Cleonidius* species, in general, appear to parallel some of the aspects of evolution of *Apleurus* species or lineages, but differ markedly in various others.

As mentioned, at least one species of *Cleonidius* is known from the Palearctic Region. However, its relationships are at present unclear (see Phylogeny section).

Unlike *Apleurus* , *Cleonidius* does not appear to be North American in origin because the Palearctic species component of *Cleonidius* appears to be sister to the Nearctic species component (Fig. 246). Thus, a Palearctic origin for the genus is to be preferred with subsequent entry into North America of this ancestral stock. It is most likely that a trans-Beringian grassland or savanna vicariance of this stock (Fig. 246), such as that proposed for the origin of *Apleurus*, resulted in the evolution of Nearctic *Cleonidius*. The evidence for this is as follows: 1, Palearctic *Cleonidius* are eastern in their distribution and are apparently associated with grassland or steppe habitat; 2, association with grasslands is widespread in *Cleonidius* (although not restricted to primitive lineages or species) (Fig. 240); 3, association with woodland, although widespread, is only in more derived species (Fig. 240) (suggestive of secondary entry into that habitat type, a hypothesis supported by patterns of host plant association); and 4, the two eastern North American species are unrelated and also of a generally more derived nature. This trans-Beringian savanna or grassland event is likely to have occurred only post-late Eocene.

Within *Cleonidius* there are five of what I consider to be main, perhaps interrelated, differences from *Apleurus*: 1, species of *Cleonidius* are known from western xerophytic conifer woodland (Fig. 240); 2, species of *Cleonidius* are known from eastern North America (Figs. 215, 229); 3, species exhibit primary host plant associations with one of a various number of plant families (Fig. 241); 4, habitat association overlap (Fig. 240), altitudinal range overlap (Fig. 233), and association with less arid habitats are high; and 5, comparison of habitat associations or altitudinal ranges with the reconstructed phylogeny does not demonstrate a clear correlation with increasingly arid habitats (Fig. 240) or with lower altitudes, respectively. These differences are certainly suggestive of a different evolutionary history, one influenced less so by shifts to increasingly arid habitats, but rather by host plant shifts, allopatric

speciation within a habitat type, and habitat shifts to both more and less arid types at both lower and higher elevations over a more extensive geographic range.

There are, however, some similarities. Distributions of three of the four species groups can be geographically centered in certain areas. The *C. erysimi* group has five of six species distributed in whole or in part in California (Fig. 257); the *C. americanus* group has six of seven species distributed in whole or in part in the southern Rocky Mountain region (Fig. 258); and, the *C. boucardi* group has three of four species in the central to southern Rocky Mountain region or central México (the most primitive being in central México) (Fig. 259). With certain restrictions, namely the question of the origin of the *C. poricollis* group, this pattern brings to mind the California-central México-southern Rocky Mountain pattern in primitive *Apleurus* (Fig. 242) because the common ancestor of the *C. boucardi* group (México) and the *C. poricollis* group (questionable origin) is sister to the *C. americanus* group (southern Rocky Mountains), the common ancestor of which is sister to the *C. erysimi* group (California).

This pattern is suggestive of similar historical processes accounting for diversification in the basal lineages of the two genera, although it is possible that in *Cleonidius* the ancestral habitat association is with sclerophyll woodland rather than grasslands or savanna for the two were undoubtedly intermixed (Axelrod 1979). As such, an Eocene to Miocene vicariance of California, southern Rocky Mountain region, and central México was likely responsible for the initial diversification within the genus (Fig. 246).

Parsimony, however, dictates preference for an association with grasslands or savanna habitat because most *C. americanus* group members have a primary association with that habitat type; *C. poricollis* and *C. erysimi* group members, although not primarily associated with grasslands, are not primarily associated with woodlands; and primitive *C. boucardi* members are associated with grasslands (Fig. 240). Furthermore, the two species associated with western xerophytic conifer woodland and the single species associated with eastern North American mesophytic evergreen forest, are more or less structurally derived and not relictual in distribution. Similarly, the other eastern North American species is also structurally derived, and although restricted in distribution, is the sister-species of a structurally similar western North American species (Fig. 236).

The best evidence, however, for association with xerophytic woodland being secondarily derived concerns host plant associations. *Cleonidius texanus* and *C. quadrilineatus* are both associated primarily with Rosaceae and Rhamnaceae and each have their two closest relatives associated exclusively with Leguminosae (Fig. 241). This, and presence of infrequent association of *C. texanus* and *C. quadrilineatus* with Leguminosae (but not of relatives on Rosaceae or Rhamnaceae), suggests Leguminosae was the plesiotypic host plant for these lineages and that Rosaceae and concomitantly association with xerophytic woodland, derived.

Indeed, the widespread distribution and abundance of species associations with Leguminosae suggests that association with this family, or an ancestral form of this family, Rosaceae and Rhamnaceae (the families are phylogenetically closely related and placed in the order Rosales [Cronquist, 1968]), may be ancestral for *Cleonidius* as a whole. Even more parsimonious, however, is the hypothesis that association with Compositae is ancestral for the genus. Association with this family is equally widespread and abundant in the genus, but unlike Leguminosae, is found particularly in plesiotypic species in the *C. erysimi*, *C. americanus*, and *C. poricollis* species groups, not in the more derived species, as is the association with Leguminosae. Association with Compositae is also known in numerous other Cleoninae (*e.g., Apleurus, Cleonis, Cyphocleonus*, some *Lixus*). Accordingly, preference must herein be given

to a plesiotypic association with Compositae, but final resolution of these competing hypotheses rests largely on determination of host plant relationships in those *Cleonidius* species in which they are as yet unknown, particularly, those of a primitive phylogenetic position and especially those of the Palearctic species component.

Further supportive of the more recent trans-Beringian vicariance of savanna or grassland are: 1, non-relictual geographic or structural status of any *Cleonidius*; 2, lack of extensive structural divergence between species perhaps indicative of less available time for evolutionary change to have occurred; and 3, likelihood that *C. vibex* and relatives are the sister group to Nearctic *Cleonidius* (see Phylogeny section).

Axelrod's (1975) Madrean-Tethyan hypothesis has not been given much support from other studies. Floras of the eastern Gulf Coast and southeastern North America do not show evidence of arid-adapted taxa (Graham, 1965). The hypothesis also does not receive any clear support from the biogeographic analyses presented herein. Clearly, I believe we must accept an ancestral association with grassland or savanna, as in *Apleurus*. Diversification in *Cleonidius*, however, has apparently been much more complex than in *Apleurus* as evidenced by: lack of a clear correlation between phylogeny and habitat association (Fig. 240); numerous different and variable habitat associations of the species (Fig. 240); different host plant associations (Fig. 241); and present relatively extensive species sympatry and altitudinal range overlap (Fig. 233).

Within species groups, caution must be exercized because degree of confidence in various of the hypothesized relationships is low (Fig. 237). Within the *C. erysimi* group, monophyly of *C. subcylindricus-C. texanus-C. longinasus* is strongly supported by three primary characters. Relationships of this lineage and the remaining three species in the species group are however much less clear and are left as an unresolved trichotomy (Fig. 237). Assuming, as noted, that the *C. erysimi* species group evolved in California (Fig. 246), it is likely that, as conditions became more arid, there was an entry into semi-desert habitat in the *C. eustictorrhinus-C. erysimi* lineage (Fig. 247). The hypothesized ancestral association with Compositae was retained in this lineage and *C. pleuralis*, and the ancestor of the *C. subcylindricus-C. texanus-C. longinasus* lineage likely shifted onto Leguminosae. *C. eustictorrhinus* and *C. erysimi* may then have diverged in part as a result of an east-west vicariance between California and the Great Basin Region with subsequent dispersal of *C. erysimi* back into California (Fig. 248). This event likely also involved, or may have even been exclusively due to, a host plant shift involving Compositae and the phylogenetically unrelated (Cronquist, 1968) Cruciferae. Evidence for this is as follows. The sister-species *C. americanus* and *C. frontalis* (of the *C. americanus* group) have similar geographic distributions to *C. eustictorrhinus* and *C. erysimi*; *C. americanus* is associated with Compositae in California; host plant associations of *C. frontalis* are not known. In *C. eustictorrhinus* and *C. erysimi* the opposite is true; the widespread *C. erysimi* is found on Cruciferae whereas plant associations of the California *C. eustictorrhinus* are not known. Furthermore, in the *C. poricollis* group, both *C. poricollis* and *C. calandroides* are associated with Cruciferae, but *C. poricollis* is also markedly associated with Compositae. Patterns of Cruciferae-Compositae association between closely related taxa therefore (and, as noted, Leguminosae-Rosaceae/Rhamnaceae associations of a similar nature), appear to repeat within *Cleonidius* (Fig. 241) and may thus represent more general patterns of host plant relationships. In view of this, association with Compositae can be hypothesized for *C. eustictorrhinus*, and association with Cruciferae for *C. frontalis*. If *C. pleuralis* ultimately proves sister-species of the *C. eustictorrhinus-C. erysimi* lineage then

evidence for *C. eustictorrhinus* being associated with Compositae is more marked, because then only one shift from Compositae in the evolution of the three species is required. Within *C. pleuralis* there has been a continued adaptation to more markedly arid lands (Fig. 240), perhaps interrelated with association with Compositae (note relatively high level of association with arid habitats in *Apleurus*, all of which are on Compositae; association of *C. poricollis*, the only other *Cleonidius* that is associated with desert habitats, is also with Compositae).

In the *C. subcylindricus-C. texanus-C. longinasus* lineage there appears to be independent entry into xerophytic and mesophytic evergreen woodlands in the central-southern Rocky Mountain region and eastern North America by *C. texanus* and *C. subcylindricus* respectively as evidenced by the pattern of host plant associations. An initial vicariance in this lineage between *C. subcylindricus* in eastern North America and the *C. texanus-C. longinasus* lineage in western North America, lineages both ancestrally on Leguminosae, was likely followed by a host plant shift from Leguminosae to Rosaceae and Rhamnaceae and concurrent shifts to xerophytic woodland habitat by *C. texanus* and to mesophytic woodland habitat by *C. subcylindricus* (Fig. 249).

Within the *C. americanus* group, most of the species are primarily associated with grasslands; *C. americanus* and *C. notolomus* are associated exclusively with Pacific semi-desert and desert-grassland transition respectively (Fig. 240). Vicariance patterns are clearly evident in the present distributions of species in this group. A California-Great Basin or southern Great Plains vicariance can be proposed to account for the origin of the *C. americanus-C. frontalis* lineage and the ancestor of the remainder of the *C. americanus* group (Fig. 250). Within the former lineage, a California-inland vicariance again very likely explains the evolution of *C. americanus* and *C. frontalis* (Fig. 251). This was likely concomitant with a shift to more arid habitats, especially by *C. americanus*.

Origins of *C. canescens* and of the *C. notolomus-C. collaris* and *C. puberulus-C. infrequens* lineages are not clear. However, a north-south vicariance of both *C. collaris* and *C. notolomus* (Fig. 253), and of *C. puberulus* and *C. infrequens* (Fig. 252), accounts for the present distribution of these species. Of the four, only *C. notolomus* has changed from a grassland association to desert-grassland transitional habitat (Fig. 240). Few structural differences between these sister-species, and the allopatric distributions favour a relatively recent occurrence of these speciation events. Association with Compositae is hypothesized as plesiotypic for the species group.

Origin of the *C. poricollis* group is unclear principally because of the widespread distribution and eurytopic nature of *C. poricollis* (Fig. 228). It was undoubtedly concurrent with the hypothesized initial radiation of species group lineages and while an east coast isolation of *C. calandroides* likely accounts for the origin of that species, it is not clear where the ancestor of *C. poricollis* and *C. calandroides* evolved. Association with Compositae is proposed as ancestral for this species group as well.

In the *C. boucardi* group, there was likely a Mexican highlands isolation of *C. boucardi* in mesquite-grassland and a southern Rocky Mountain isolation of the *C. trivittatus-C. quadrilineatus-C. placidus* lineage in grassland habitat, an event brought about by increasing aridity and the formation of intermediate desert-grassland transitional or semi-desert habitats (Fig. 254). In the *C. trivittatus-C. quadrilineatus-C. placidus* lineage, in which association was likely with Leguminosae, an east-west vicariance of *C. trivittatus* and *C. quadrilineatus-C. placidus* in grassland and semi-desert habitats respectively, appears to account for the origin of *C. trivittatus* (Fig. 255). Subsequent entry into xerophytic evergreen woodland habitat by the

semi-desert adapted ancestor, which, as in the *C. erysimi* group, continued to be associated with Leguminosae, resulted in *C. quadrilineatus* in the eastern xerophytic woodlands and *C. placidus* in the semi-desert habitat of California (Fig. 256). Concurrent with this habitat shift by *C. quadrilineatus* was a host plant shift to Rosaceae and Rhamnaceae; *C. placidus* continued to be associated with Leguminosae. Present occurrence of *C. quadrilineatus* in California is likely a recent dispersal event. Ancestral host plant relationships of this group are also likely with Compositae.

Summarizing, both *Apleurus* and *Cleonidius* are hypothesized to have entered North America in savanna or grassland habitats (or their precursors) across Beringia during late Eocene time. In both genera there appears to be an initial association with Compositae and vicariance of lineages in grassland or mesquite-grassland between California, central México, and the southern Rocky Mountains. Further speciation event in *Apleurus* appear due primarily to shifts to apotypic habitat types brought about by increased aridity during the later Tertiary; there is little within habitat-type allopatric speciation. Host plant shifts are not a factor, for all *Apleurus* species remain associated with Compositae. Host plant shifts, however, primarily between Leguminosae-Rosaceae and Compositae-Cruciferae, and, to a lesser degree, within-habitat-type allopatric speciation, appear to predominate as the causes of further speciation in *Cleonidius*, most species of which remain associated with plesiotypic less-arid habitat types such as grasslands and desert-grasslands.

Evolutionary trends and adaptations

Adaptive trends to arid conditions

Numerous apparent adaptations to arid habitats are known in Coleoptera, including Curculionidae (Crowson, 1981). Some of these are exhibited in Cleoninae.

Wing length and flightlessness.— Adults of various species of North American Cleoninae are apterous or brachypterous to varying degrees and in varying frequency. Some, such as *Stephanocleonus confusus* or *Apleurus aztecus*, have the elytra more or less solidly fused together along the median suture. The cuticle is also thick and hard in many of these same individuals. Flightlessness appears more frequenty in traditional Cleonini than in traditional Lixini.

In *Apleurus* no clear phylogenetic trend is evident in this character although adults of the closely related *A. angularis*, *A. jacobinus* and *A. porosus* are all more or less apterous. Lack of a trend in *Apleurus* is perhaps surprising in view of the correlation of phylogenetic position with occupation of increasingly arid habitats (Fig. 238). Similarly, in *Cleonidius*, there is no clear phylogenetic trend in this character. Adults of species of the *C. americanus* group are predominantly brachypterous but they are mostly associated with grassland habitats and not more arid habitats. Undoubtedly, degree of aridity is not the sole Undoubtedly, degree of aridity is not the sole factor influencing the frequency of brachyptery and although the aforementioned adaptations may serve to prevent desiccation in arid environments, the spatial distribution of the habitat-type or of host plants, likely also influences the tendency towards or away from brachyptery. Compromise between these differing selective forces likely results in the wing-length polymorphisms noted in some species and the lack of a clear trend.

In species in the southwestern United States, populations on both sides of the Continental Divide, in which individuals are flightless, are structurally more distinct in the north, where the divide is high in elevation, as compared to the south, where the divide is low in elevation and where gene flow seems likely. Species exhibiting similar distributions but which are composed

of macropterous individuals do not show such patterns of variation.

Diel activity.— There is no evidence to indicate distinct peaks of diel activity in North American Cleoninae which might indicate avoidance of diurnal stressful conditions in an arid habitat. Such diel activity is known in other arid land Curculionidae (C.W. O'Brien, E.L. Sleeper, pers. comms.).

Burrowing adaptations.— Modifications of legs for burrowing are not known in North American Cleoninae. This is not surprising in view of 2, above. There are, however, adults of some species that possess long erect surface vestiture which may prove correlated with life on sand dunes and which may facilitate movement through sandy substrates. Such long vestiture is known in various obligate sand dune Scarabaeidae and other Curculionidae.

Ventral tarsal pilose vestiture.— Within *Apleurus* (Figs. 234–235), and to a lesser extent also in *Cleonidius* (Figs. 236–237), a clear trend is evident towards reduction in ventral tarsal pilose vestiture. This reduction has been reasonably suggested to be due to living predominantly on the ground rather than on plants (Kissinger, 1964; Crowson, 1981) and is widespread in many arid-adapted Curculionidae. In *Apleurus* the trend is as expected, because those more derived species in more arid environments, where plants are more widely spaced, and where it is less desirable to spend time exposed on the plant, lack ventral tarsal pilose vestiture or have pilose pads that are markedly reduced. In *Cleonidius* however, this is not clearly so, for although more arid habitat species (*e.g., C. erysimi*) possess reduced pilose pads, it is the members of the *C. americanus* group which exhibit the greatest frequency of lack of ventral tarsal pilose vestiture. This is perhaps surprising, for the species in this group are associated principally with plesiotypic grassland habitats; predicted adaptive correlates are thus not always evident in *Cleonidius*.

Other evolutionary trends

Host plant associations.— No trends in host plant relationships are evident in *Apleurus*, because all species appear associated with Compositae (Fig. 239). In *Cleonidius* however, two repeated patterns warrant mention (Fig. 241). Leguminosae-Rosaceae/Rhamnaceae associations are found in the sister-species *C. longinasus-C. texanus* and *C. placidus-C. quadrilineatus*, and Compositae-Cruciferae associations are found in *C. poricollis-C. calandroides* and are hypothesized in *C. americanus-C. frontalis* and *C. eustictorrhinus-C. erysimi*. It is unlikely that the Compositae-Cruciferae association is phylogenetically based, but rather reflects the co-occurence (perhaps recent) of these two plant taxa in the same, more arid habitats. The Leguminosae-Rosaceae/Rhamnaceae association, however, is likely phylogenetically based for the taxa involved are closely related and the host plant shift is concomitant with a shift in habitat association.

Groups in which sympatry is low, altitude range overlap low, and habitat association overlap low, tend to have species which differ little in host plant relationships. Increasing levels of these factors appear to be correlated with more varied host associations. Host plant associations, largely unknown in the *C. americanus* group, can thus be predicted to vary little in terms of their taxonomic range and thus largely be with Compositae or Cruciferae.

There is no trend from generalist to specialist feeding in either *Apleurus* or *Cleonidius*.

Habitat associations.— As noted in detail in the biogeography section, there is a clear trend in *Apleurus* for phylogenetically more derived species to be associated with increasingly arid habitats (Fig. 238) and lower elevations. This is not so in *Cleonidius* wherein most species are associated with grassland or grassland-desert habitats (Fig. 240).

Size.— Within *Apleurus* there is a tendency towards increased size (Figs. 234–235); such is not clearly evident in *Cleonidius*. Increased size in an arid environment may serve to aid in prevention of water loss for surface area to volume ratios would be lower in larger individuals which are, notably, found in more arid environments. In *Cleonidius* however, the largest species are those in the *C. boucardi* group. These are not found in notably arid habitats but rather grasslands, semi-desert and xerophytic evergreen woodlands.

Genitalia.— Form of male genitalia including the internal sac is very conservative in species of both *Apleurus* (Figs. 99–104) and *Cleonidius* (Figs. 177–196) and form of female genitalia is very conservative in *Cleonidius* (Figs. 157–176). Such is not so in females of *Apleurus* wherein there is a clear trend towards reduction in size of the stylus on gonocoxite II and an increasingly subapical position of attachment of the same (Figs. 89–96). This trend is likely related to the oviposition habits of the species but such are not known in detail for any North American species of Cleoninae.

Form of the aedeagus (Figs. 31–36) and of the internal sac (Figs. 43–48) differs markedly between species of *Stephanocleonus*, in contrast to the lack of differences in *Cleonidius* and *Apleurus*. Reasons for this are unknown.

Elytral scale patterns.— Elytral scale patterns are generally uniform within and between *Apleurus* species except for *A. angularis* (Figs. 72–74) and *A. albovestitus* (Figs. 75–79) wherein various forms are recognizable. Correlation of particular scale patterns with geographic distribution suggests a local adaptive significance, one I believe associated with crypsis on the ground substrate or in debris under host plants. A thermoregulatory role however, may apply to those *A. albovestitus* in the lower Colorado River drainage. In *Apleurus* there are no species which possess a distinctly vittate scale pattern; most are more or less mottled in general appearance.

In *Cleonidius* elytral patterns vary between species but not to a significant extent within a species (with the exception of *C. canescens*). Adaptive significance of the vittate pattern (*e.g.,* Fig. 131) found in most *Cleonidius* is likely one of concealment on host plants or in debris under the host plant. Crypsis on the ground substrate is not likely, except perhaps in the *C. americanus* group, for otherwise, most species have moderately developed ventral tarsal pilose vestiture indicating life predominantly on plants. Only in the *C. americanus* group is there predominance of species in which individuals have reduced ventral tarsal pilose vestiture. Also in this group are found the only species with mottled elytral scale patterns (*e.g.,* Figs. 124–125). These patterns are similar to those of *Apleurus* species, and likely serve as an adaptation to life on the ground substrate.

Vittate (and margined [Figs. 118–123]) patterns predominate in species of *Cleonidius* with extensive ventral tarsal pilosity; non-vittate patterns predominate in species with reduced tarsal vestiture. Wide ranging species with reduced ventral pilose tarsal vestiture in *Apleurus* exhibit geographic variation in scale pattern, whereas restricted species or those wide-ranging species with extensive ventral pilose vestiture do not show variation in elytral scale pattern. In *Cleonidius* nearly all species exhibit little or no variation in elytral scale pattern (except for *C. canescens* of the *C. americanus* group, which like *A. angularis*, has more or less vittate and non-vittate forms occurring on the west and east sides of the Continental Divide). Within the *C. americanus* group, which contains mostly allopatric species with reduced ventral vestiture, there is the most extensive within-species-group variation in scale pattern. Other species groups do not show within group variation in scale pattern. It thus appears that there is an inverse correlation in both *Apleurus* and *Cleonidius* between degree of variation in elytral pattern and

extent of ventral tarsal pilose vestiture, but only seen in species or species groups distributed over large geographic areas.

Patterns and predictions

From results of this study of Cleoninae, some tentative generalizations can be made as regards arid adapted faunas in North America.

1. Preference must go to a post-late Eocene vicariance of savanna or grassland habitat, or precursory habitat, across Beringia as the original mode of isolation of Nearctic arid land taxa which possess Palearctic relatives also inhabiting arid lands (Figs. 242, 246). There is no evidence for direct Madrean-Tethyan connections as proposed by Axelrod (1975).

2. The most plesiotypic species or lineages in the Nearctic region will be found on Compositae in various combinations of the mesquite-grasslands of the highlands of central México, the southern Rocky Mountain grasslands, and in one of various habitats in California which may be relictual or predominantly grassland in nature (Figs. 242, 246).

3. Arid-adapted species in eastern North America are more recent in origin, not relictual, and are related to a species or a lineage of few species in western North America.

4. California is the geographical area recognizable as possessing the most arid land endemics. All have their closest relatives outside of California.

5. Evolution in arid-adapted taxa may involve a trend toward occupation of increasingly arid habit by successively more derived species (Fig. 238). This is accompanied by few or no host plant shifts (Fig. 239), and may be limited to non-speciose groups. Sympatry, altitudinal range overlap, and habitat association overlap is low in these taxa.

6. Alternatively to 5 above, host plant shifts (Fig. 241) permit sympatry, altitudinal range overlap and habitat association overlap and are perhaps associated only with more speciose groups. No clear correlation between phylogenetic position of the species and degree of aridity of habitat occupied is evident (Fig. 240).

7. Species inhabiting North American desert habitats are of recent origin (but not necessarily of derived phylogenetic position), and are related to taxa associated with precursory North American non-desert habitats although not in a generally predictable manner. That regional deserts are composed of taxa from non-desert arid habitats and are of recent origin is supported. No regional desert endemics are known in *Apleurus* or *Cleonidius* .

8. Contrary to statements of other authors (Axelrod, 1985), grassland endemics are known, are primitive or derived in their phylogenetic position, and should thus be expected in other arid land adapted taxa.

9. Compositae-Cruciferae and Leguminosae-Rosaceae/Rhamnaceae host plant shifts may represent general patterns to be found in other phytophagous taxa that feed on vegetative plant structures. Shifts from Leguminosae to Rosaceae and Rhamnaceae may prove generally associated with entry into western upland xerophytic evergreen woodland habitat by some phytophagous taxa. These shifts appear to have a phylogenetic basis as indicated by the fact that the families are placed in the order Rosales (Cronquist, 1968).

In contrast, Compositae-Cruciferae host plant shifts are likely due to occurrence of both the two plant and two weevil taxa in the same habitat types. No phylogenetic basis can be inferred because the two families are not apparently phylogenetically closely related as indicated by their placement in separate, unrelated subclasses (Cronquist, 1968).

CONCLUSIONS AND FUTURE RESEARCH

Scientific studies should not only attempt to answer specific questions but should also strive to pose questions which might prove the basis for further inquiry. More than anything else, I believe this study draws attention to the need for examination of world faunas or at the least, regional faunas placed in a world perspective. Traditionally, North American Cleonini have all been treated as *Cleonis*, but as now should be clearly evident, the relationships of many taxa in North America are actually quite phylogenetically distant.

Relationships of *Apleurus* are largely resolved. Unfortunately, this cannot be said with the same confidence for *Cleonidius*. World study of the speciose and structurally diverse genus *Lixus* should help resolve the still problematical relationships and even species constituency of *Cleonidius*. What other Old World *Lixus* may require placement in *Cleonidius* and subsequent study of large numbers of individuals of these species and determination of what their relationships are to North American *Cleonidius*, should help to resolve the phylogenetic placement of the Old World *Cleonidius* , further resolve the interrelationships of North American species, and answer some still remaining questions of biogeographic importance. This will be a large task, for within *Lixus* are placed a great number of species. More complete knowledge of structural diversity of *Lixus* species and the phylogenetic relationships of component species-groups or subgenera should ultimately lead to a clearer understanding of suprageneric relationships in Cleoninae and a well substantiated tribal classification.

Not to be forgotten are the interrelationships among genera of traditional Cleonini. A start at a study of these relationships leading, I hope, to a generic reclassification, has been made as part of this present study. Results are not presented in detail here; only characters of relevance to our understanding of the North American fauna have been included. Study of representatives of generic-group names not yet examined is required, as is study of more species in more speciose genera to assure proper placement and uniformity of features that appear to prove phylogenetically valuable at the generic level.

Even within the North American fauna itself, work remains to be done. For *Apleurus* and *Cleonidius* , I feel confident that no new species will be discovered; for *Stephanocleonus* , largely because the genus is northern and Holarctic, I suspect that one or more new species remain to be discovered, perhaps in the Yukon Territory and Alaska. Whether any of the North American species are Holarctic in distribution (and perhaps conspecific with nominal Old World species) also needs to be determined for it has not been possible to examine types or representatives of even a small number of the many Palearctic species. Only when this has been done can phylogenetic relationships of the species in this genus be reconstructed.

For all Cleoninae, more host plant information needs to be compiled. Hosts, even plant associations, are not known for *Stephanocleonus* species; the relationship with Compositae needs to be further substantiated in *Apleurus* species; and, various of the species of *Cleonidius* do not have hosts or even plant associations established, and those that are established need variable degrees of further supportive data. With host plant shifts appearing to play an integral role in *Cleonidius*, more such information can only increase understanding of the evolution of species in that genus and determine whether predictions about specific host plant relationships made herein, and whether predictions that these patterns are repeated and general are borne out.

Immature stages of Cleoninae are largely unknown and unstudied. Collection and study of eggs, larva and pupae, particularly in North America, may provide characters of phylogenetic

use in substantiating relationships as based on adult characters, or, in resolving problematical relationships or those in which confidence is low.

ACKNOWLEDGMENTS

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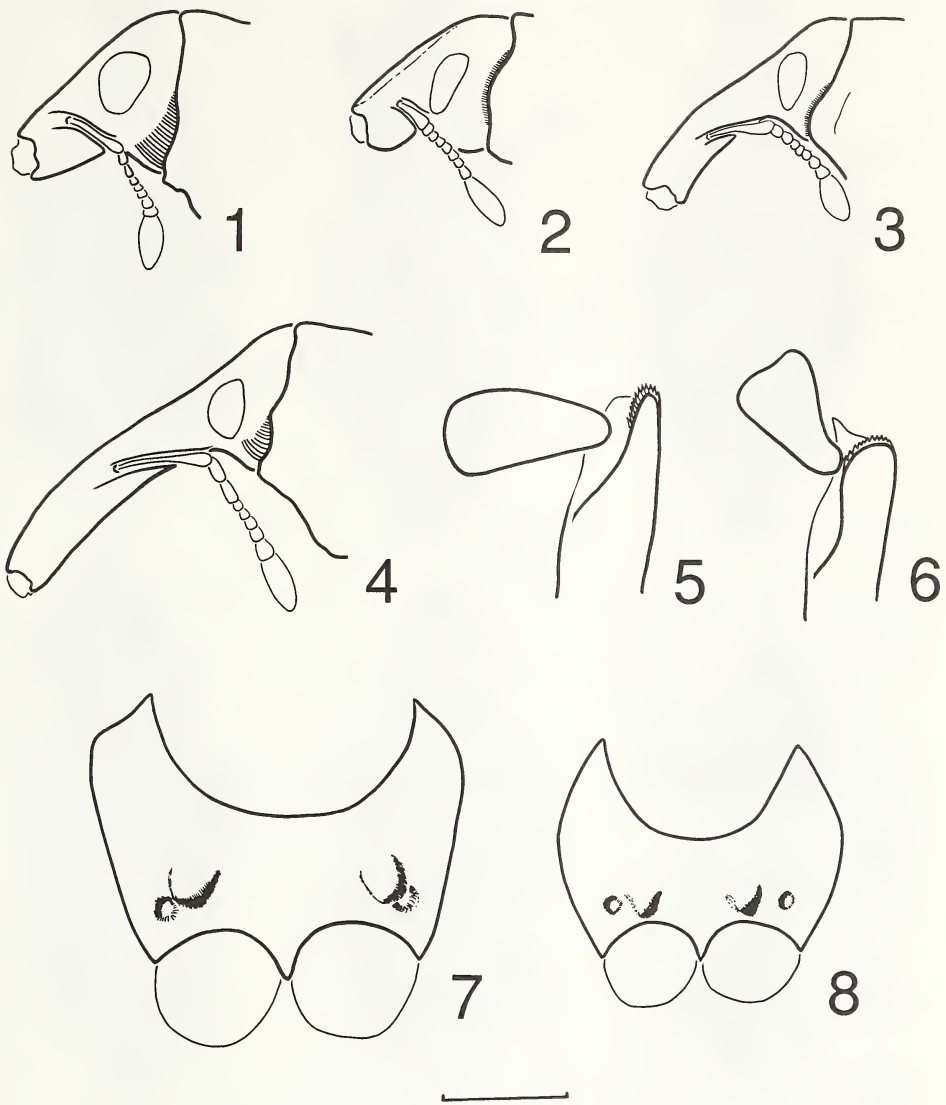
Figures 1–4. Lateral view of head of various Cleoninae. 1, *Microlarinus* species (Scale bar = 0.8 mm); 2, *Rhinocyllus conicus* (Scale bar = 1.6 mm); 3, *Larinus planus* (Scale bar = 1.6 mm); 4, *Lixus scrobicollis* (Scale bar = 1.6 mm). Figures 5–6. Apex of tibia of various Cleoninae (Scale bar = 0.5 mm). 5, *Cleonidius infrequens*; 6, *Apleurus lutulentus*. Figures 7–8. Ventral view of prosternum of various Cleoninae (Scale bar = 1.6 mm). 7, *Apleurus* species; 8, *Cleonidius* species.
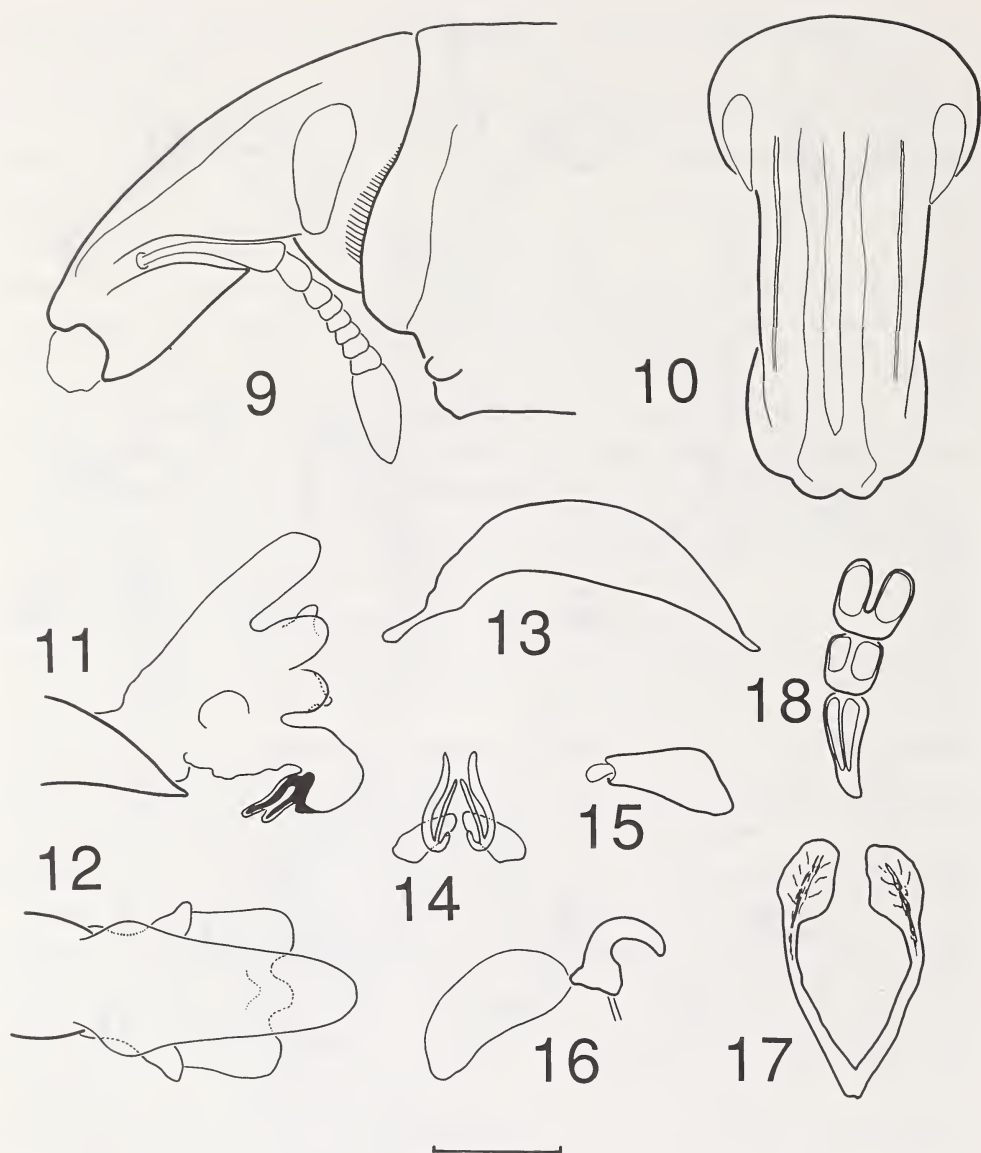
Figures 9–18. *Cleonis pigra*. 9, lateral view of head (Scale bar = 1.1 mm); 10, dorsal view of head (Scale bar = 1.1 mm); 11, lateral view of internal sac of male (Scale bar = 0.7 mm); 12, dorsal view of internal sac of male (Scale bar = 0.7 mm); 13, lateral view of aedeagus of male (Scale bar = 1.3 mm); 14, ventral view of apical sclerite complex of internal sac of male (Scale bar = 0,6 mm); 15, lateral view of gonocoxite II and stylus of female (Scale bar = 1.3 mm); 16, spermatheca of female (Scale bar = 0.7 mm); 17, ventral view of sternum VIII of female (Scale bar = 1.3 mm); 18, ventral view of metatarsus (Scale bar = 1.3 mm).
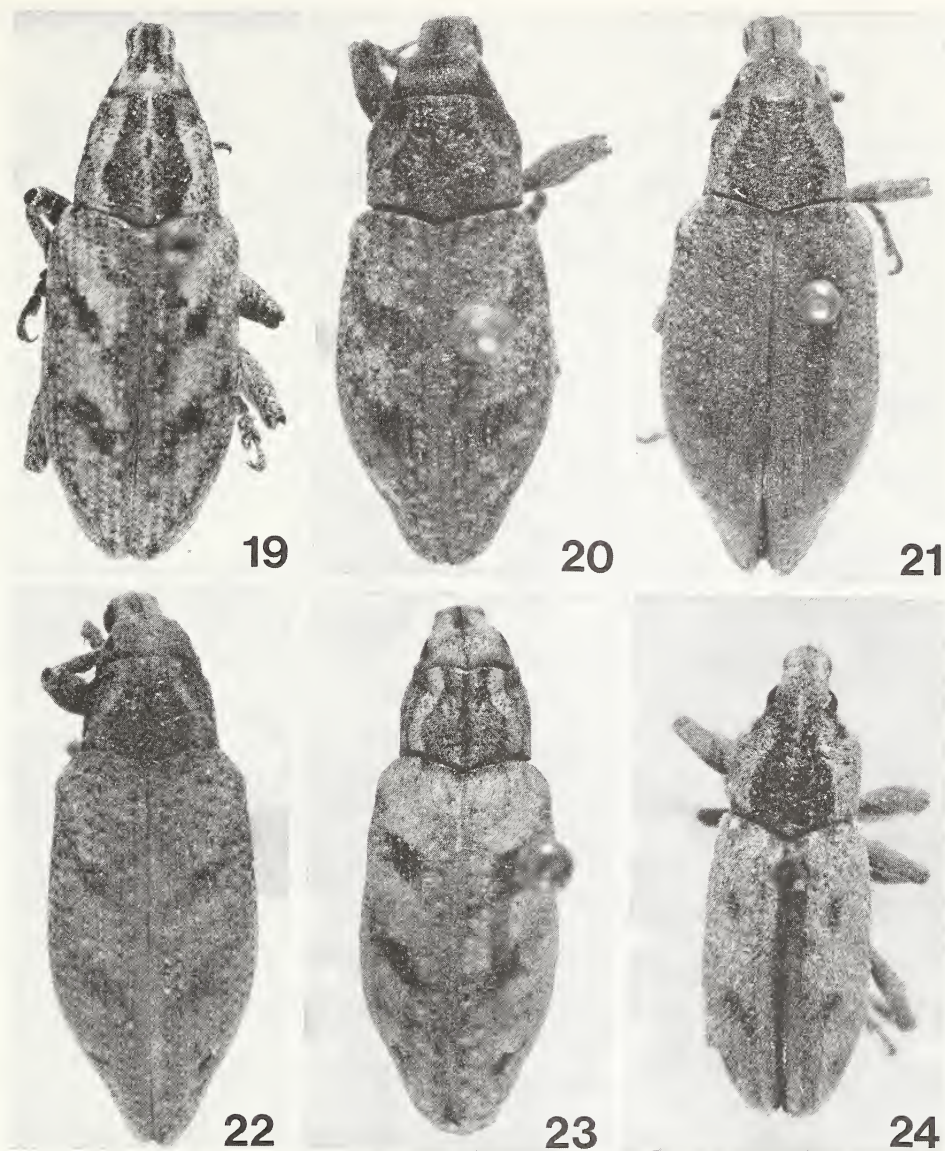
Figures 19–24. Dorsal habitus of: 19, *Cleonis pigra* (Scale bar = 5.0 mm); 20, *Stephanocleonus confusus* (Scale bar = 5.0 mm); 21, *S. immaculatus* (Scale bar = 5.0 mm); 22, *S. plumbeus* (Scale bar = 5.0 mm); 23, *S. stenothorax* (Scale bar = 5.0 mm); 24, *Apleurus (Gibbostethus) hystrix* (Scale bar = 2.5 mm).
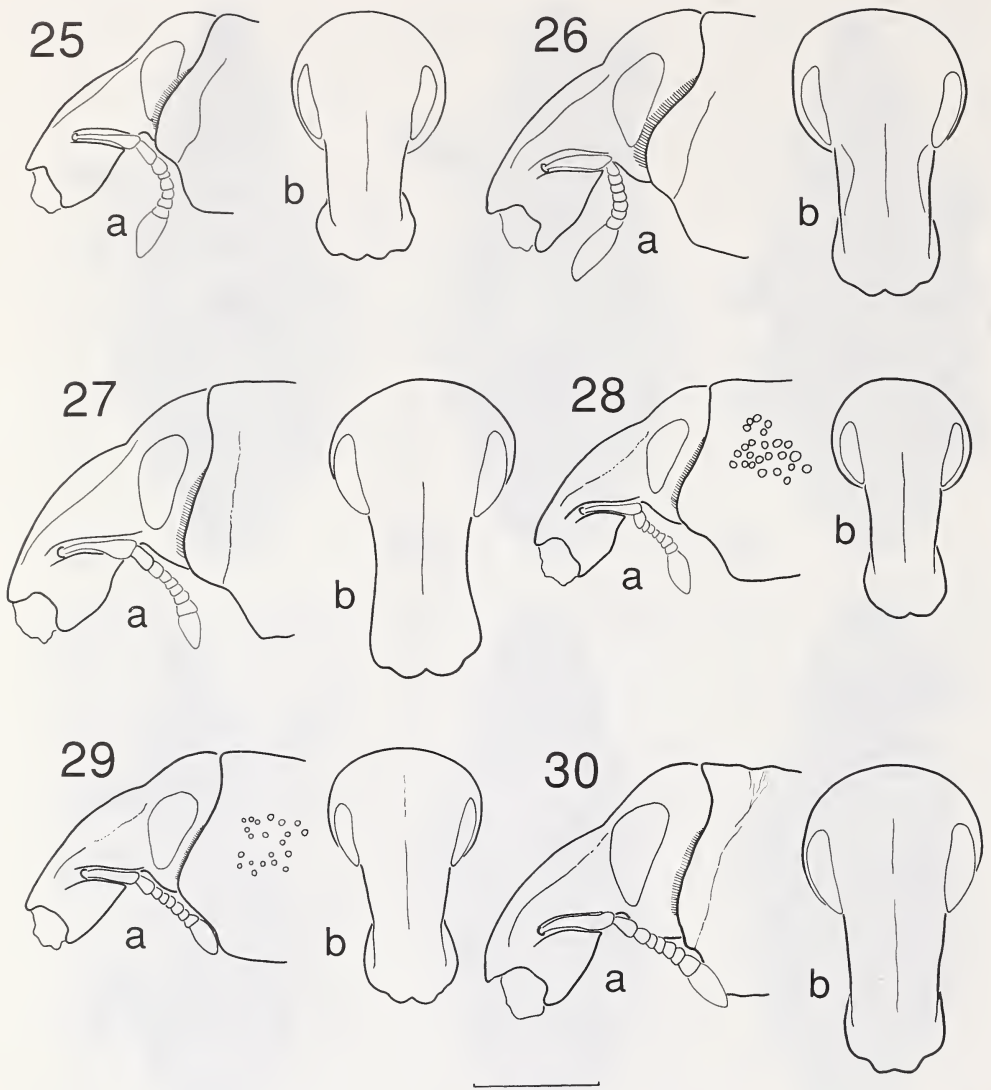
Figures 25–30. Head of *Stephanocleonus* species (Scale bar = 2.4 mm) – a, lateral view; b, dorsal view. 25, *S. confusus*; 26, *S. cristaticollis*; 27, *S. immaculatus*; 28, *S. parshus*; 29, *S. plumbeus*; 30, *S. stenothorax*.
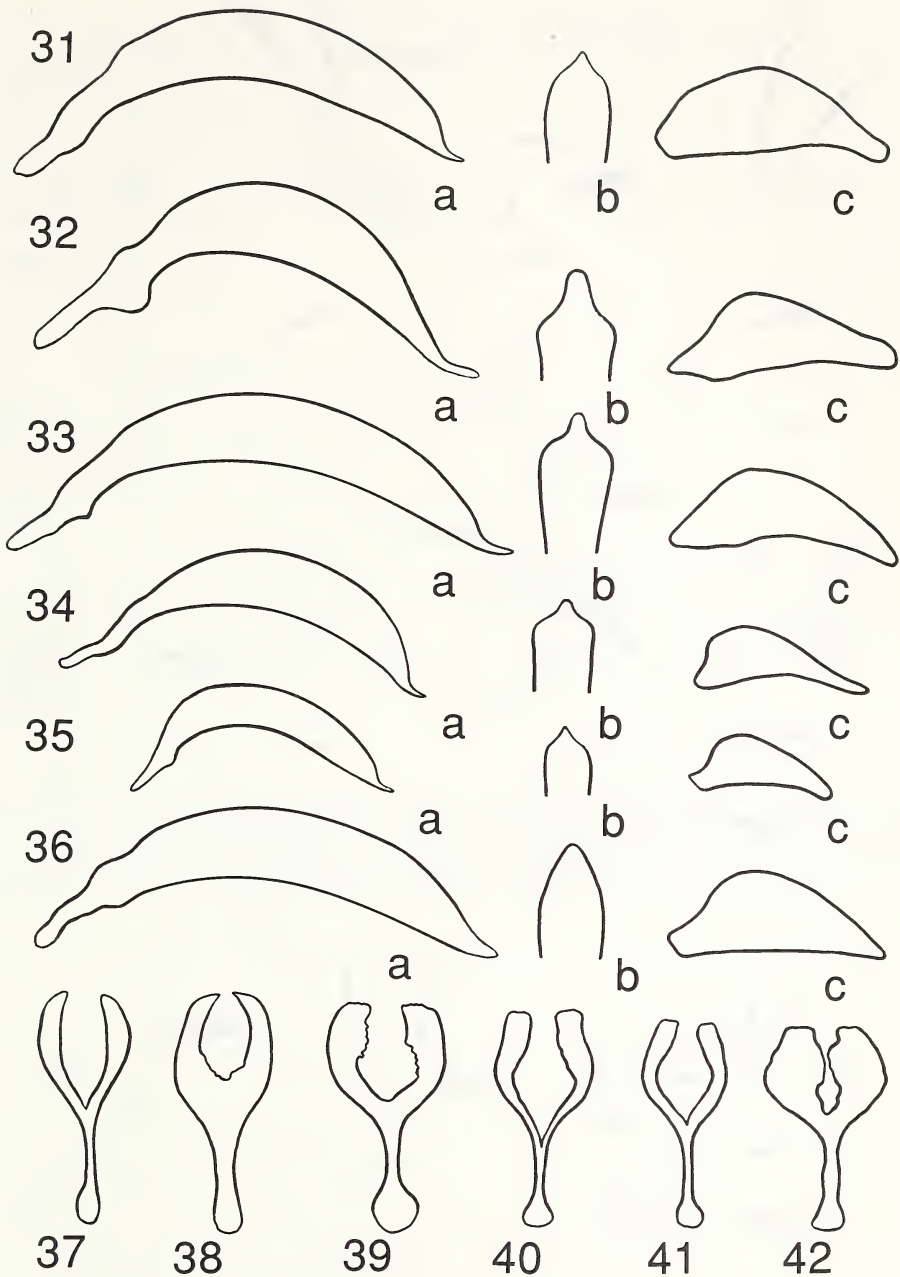
Figures 31–36. Male genitalia of *Stephanocleonus* species (Scale bar = 1.3 mm) – a and b, lateral and ventral views of aedeagus, respectively; c, ventral view of sternum VII. 31, *S. confusus*; 32, *S. cristaticollis*; 33, *S. immaculatus*; 34, *S. parshus*; 35, *S. plumbeus*; 36, *S. stenothorax*. Figures 37–42. Ventral view of sternum VIII of female *Stephanocleonus* species (Scale bar = 1.3 mm). 37, *S. confusus*; 38, *S. cristaticollis*; 39, *S. immaculatus*; 40, *S. parshus*; 41, *S. plumbeus*; 42, *S. stenothorax*.
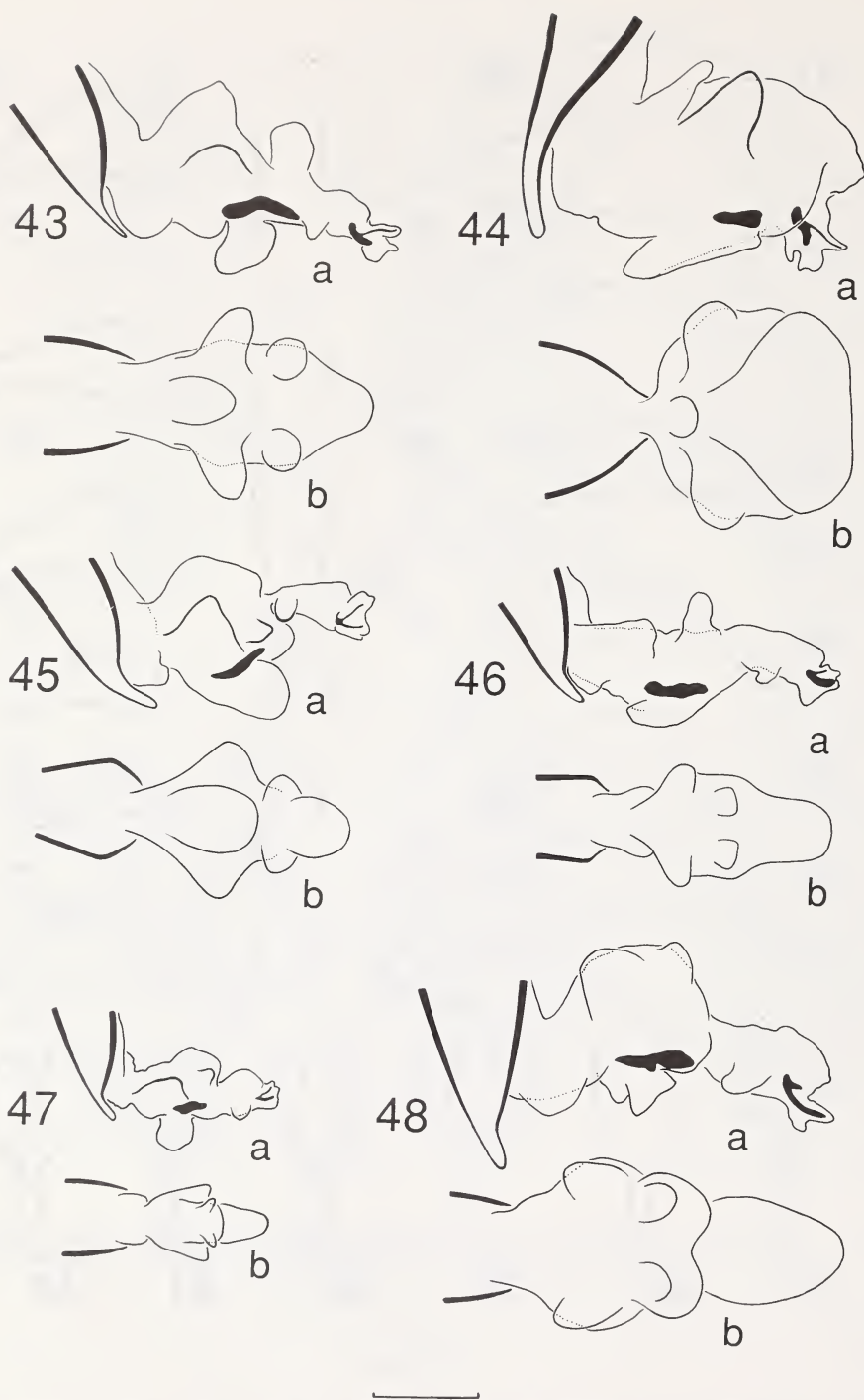
Figures 43–48. Internal sac of male *Stephanocleonus* species (Scale bar = 0.7 mm) – a and b, lateral and dorsal view, respectively. 43, *S. confusus*; 44, *S. cristaticollis*; 45. *S. immaculatus*; 46, *S. parshus*; 47, *S. plumbeus*. 48, *S. stenothorax*.
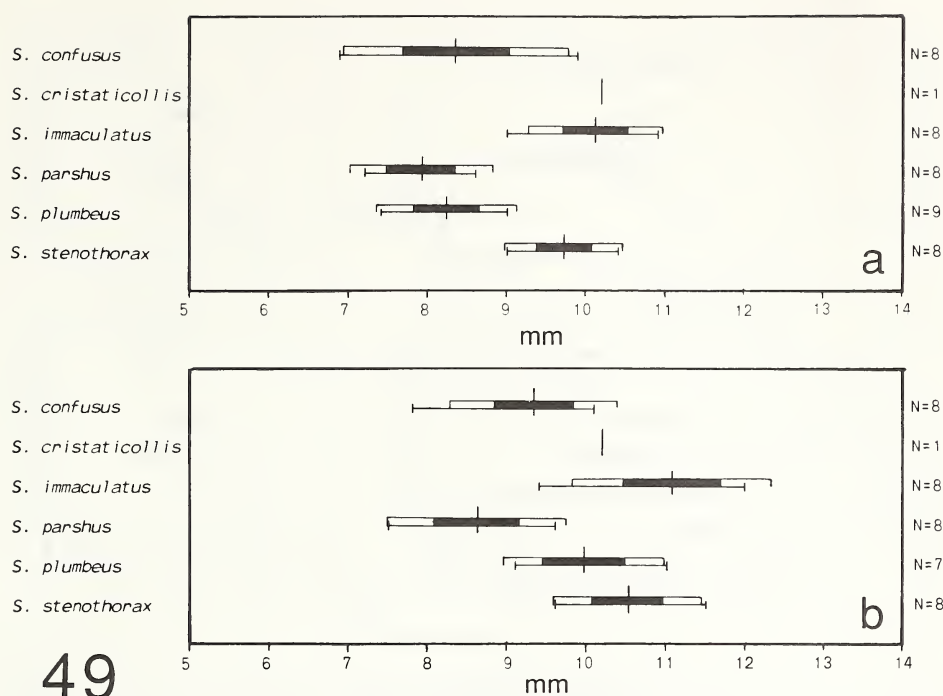
Figure 49. Hubbs-Hubbs diagram illustrating variation among specimens of *Stephanocleonus* species: length of elytra (LEI) – a, males; b, females. The range of each species is indicated by a horizontal line and the mean by a long vertical line. A solid rectangle represents two standard errors on either side of the mean and a hollow rectangle represents 1.5 standard deviations on either side of the mean. Only mean and range are shown for samples with less than five specimens.
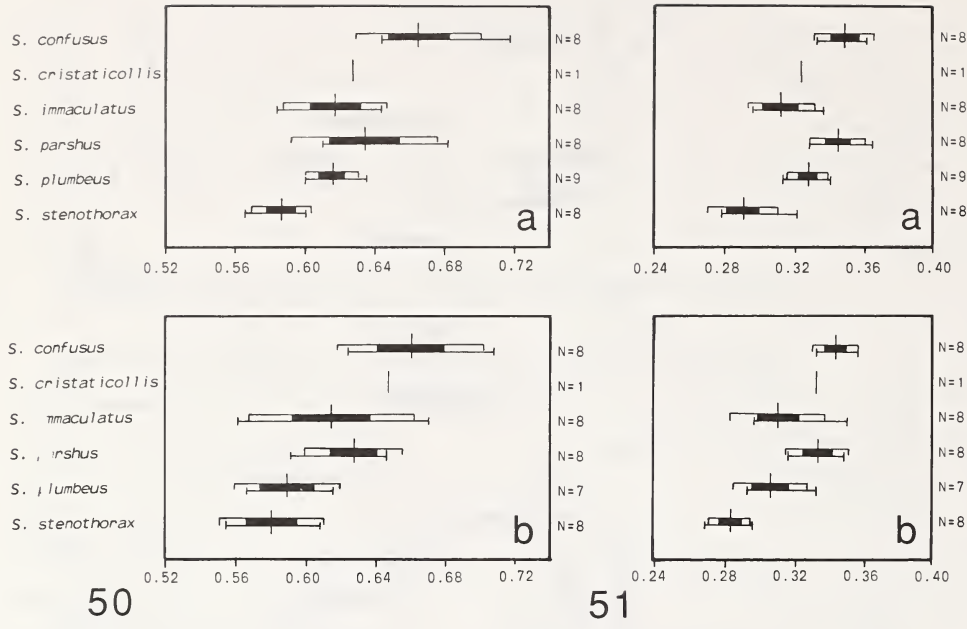
Figures 50–51. Hubbs-Hubbs diagrams illustrating variation among specimens of *Stephanocleonus* species – a, males; b, females. See caption for Fig. 49 for explanation. 50, form of elytra (WElM/LEl); 51, relative length of pronotum compared to elytra (LP/LEl).
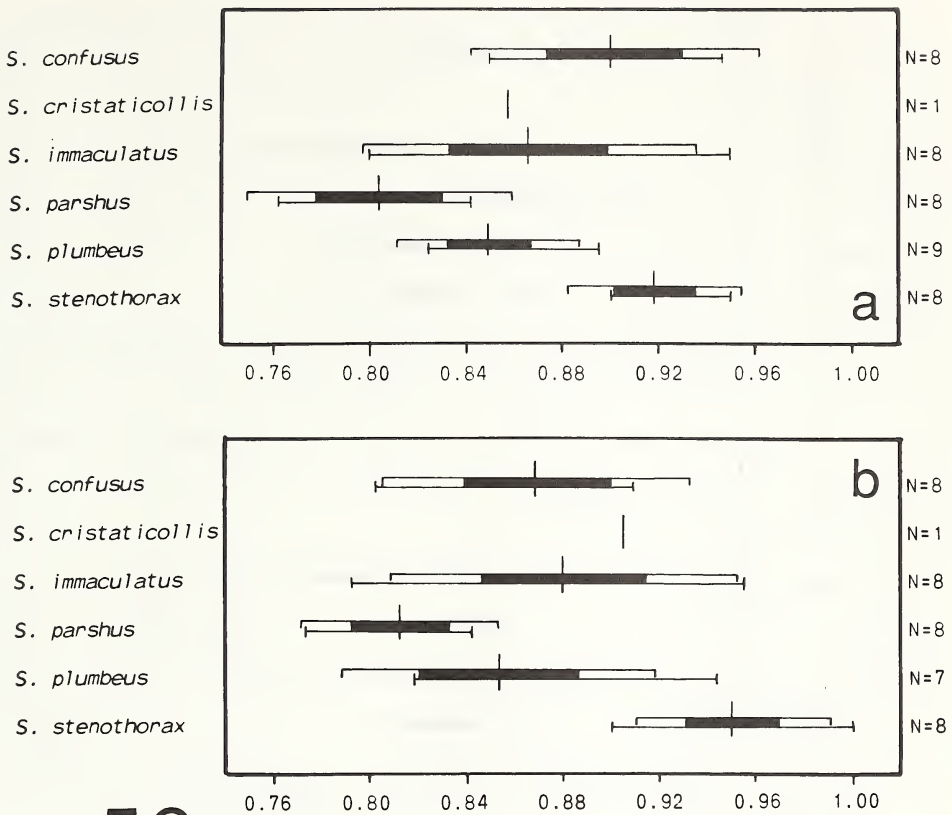
Figure 52. Hubbs-Hubbs diagram illustrating variation among specimens of *Stephanocleonus* species: form of rostrum (WRA/WF) – a, males; b, females. See caption for Fig. 49 for explanation.
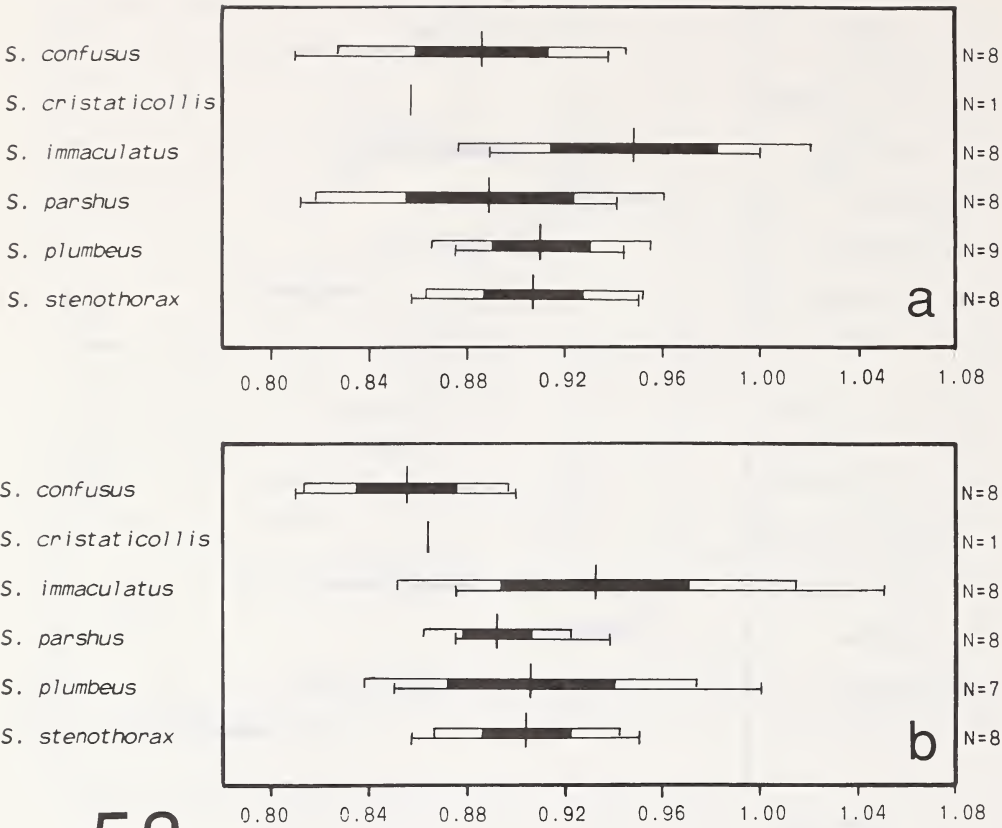
Figure 53. Hubbs-Hubbs diagram illustrating variation among specimens of *Stephanocleonus* species: relative width of frons compared to rostrum (WRA/WF) – a, males; b, females. See caption for Fig. 49 for explanation.
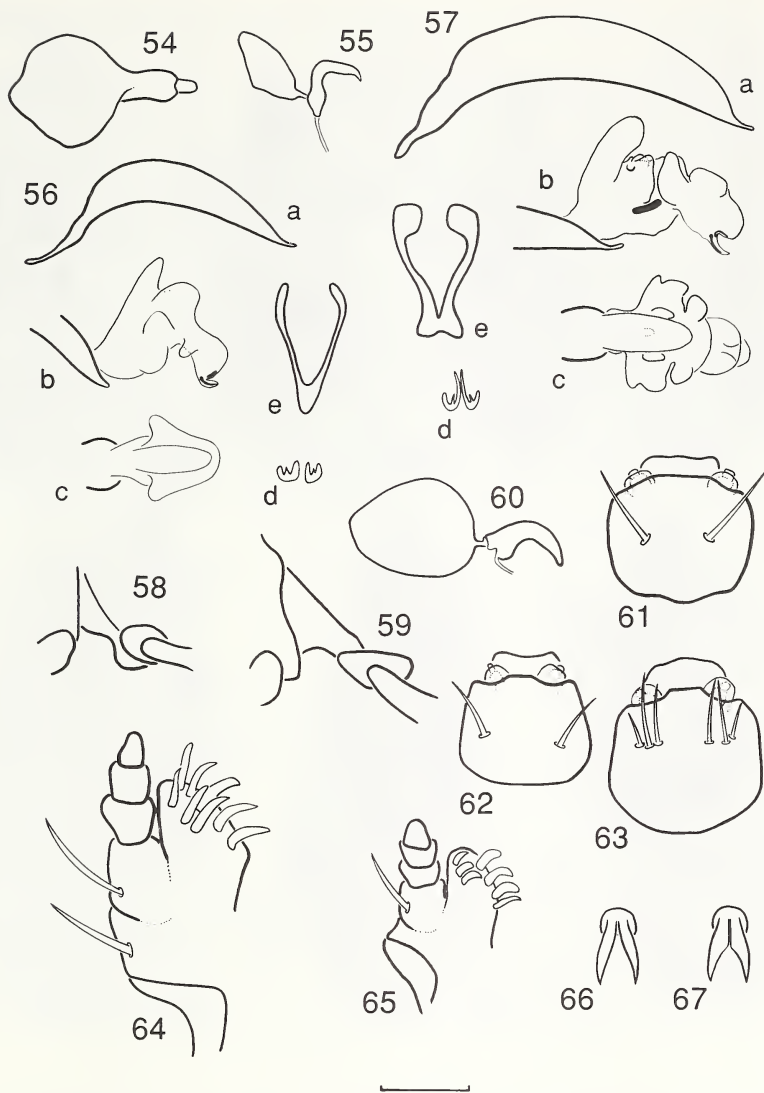
Figures 54–67. 54, lateral view of gonocoxite II and stylus of female *Stephanocleonus* (Scale bar = 0.7 mm). 55, spermatheca of female *Stephanocleonus* (Scale bar = 0.7 mm). 56, genitalia of *Chromoderus fasciatus*; a, lateral view of aedeagus of male (Scale bar = 1.3 mm); b, lateral view of internal sac of male (Scale bar = 0.7 mm); c, dorsal view of internal sac of male (Scale bar = 0.7 mm); d, ventral view of apical sclerite complex of internal sac of male (Scale bar = 0.6 mm); e, ventral view of sternum VIII of female (Scale bar = 1.3 mm). 57, genitalia of *Cnemodontus limpidus*; a, lateral view of aedeagus of male (Scale bar = 1.3 mm); b, lateral view of internal sac of male (Scale bar = 0.7 mm); c, dorsal view of internal sac of male (Scale bar = 0.7 mm); d, ventral view of apical sclerite complex of internal sac of male (Scale bar = 0.6 mm); e, ventral view of sternum VIII of female (Scale bar = 1.3 mm). 58, lateral view of mesosternum of *Apleurus (Gibbostethus) hystrix* (Scale bar = 1.3 mm). 59, lateral view of mesosternum of *Apleurus (Apleurus) lutulentus* (Scale bar = 1.3 mm). 60, spermatheca of female *Apleurus* (Scale bar = 0.7 mm). 61, ventral view of ligula of *Apleurus (Gibbostethus) hystrix* (Scale bar = 0.2 mm). 62, ventral view of ligula of *Apleurus (Apleurus) lutulentus* (Scale bar = 0.4 mm). 63, ventral view of ligula of *Apleurus (Apleurus) saginatus* (Scale bar = 0.4 mm). 64, ventral view of maxilla of *Apleurus (Apleurus) saginatus* (Scale bar = 0.4 mm). 65, ventral view of maxilla of *Apleurus (Gibbostethus) hystrix* (Scale bar = 0.4 mm). 66, tarsal claws of *Apleurus angularis* (Scale bar = 0.7 mm). 67, tarsal claws of *Apleurus jacobinus* (Scale bar = 0.7 mm).
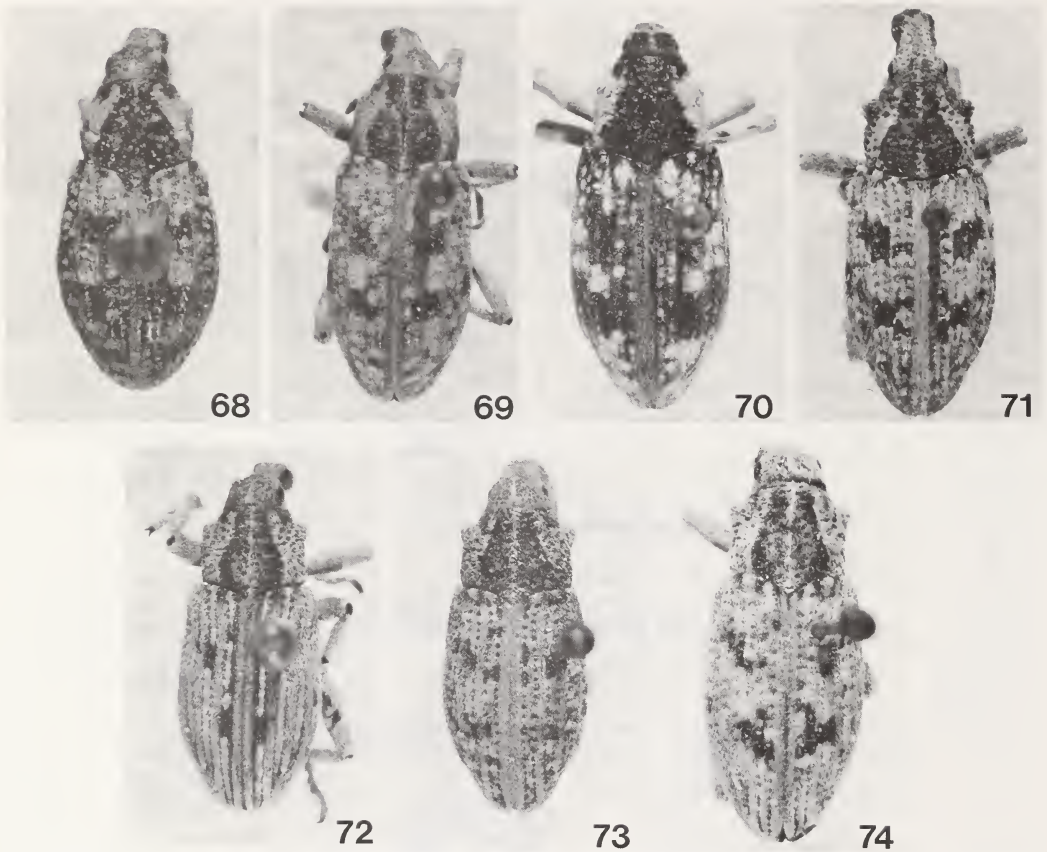
Figures 68–74. Dorsal habitus of species of *Apleurus*. 68, *A. aztecus* (Scale bar = 2.0 mm); 69, *A. lutulentus* (Scale bar = 4.0 mm); 70, *A. porosus* (Scale bar = 4.0 mm); 71, *A. jacobinus* (Scale bar = 4.0 mm); 72, *A. angularis* (3 mi. N Baker, Nevada) (Scale bar = 4.0 mm); 73, *A. angularis* (Colorado Springs, Colorado) (Scale bar = 4.0 mm); 74, *A. angularis* (Baboquivari Mountains, Arizona) (Scale bar = 3.0 mm).
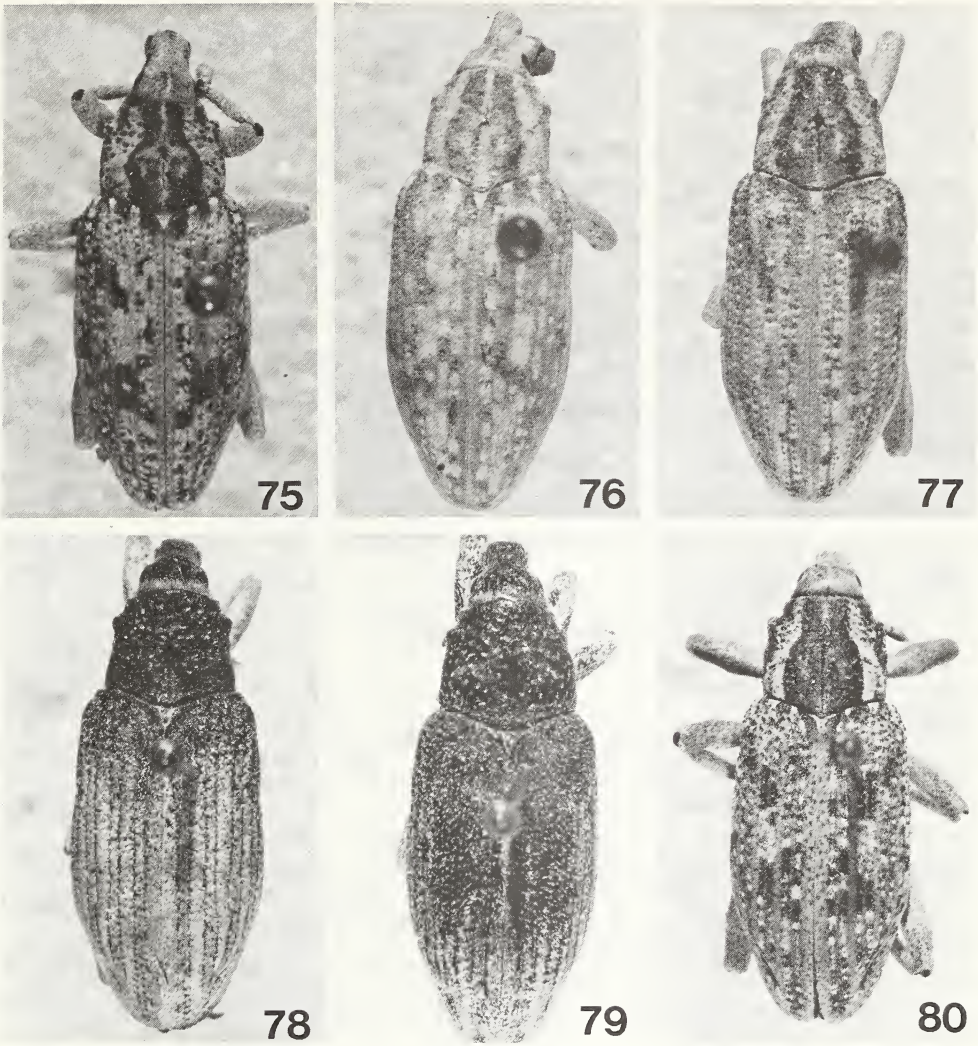
Figures 75–80. Dorsal habitus of species of *Apleurus* (Scale bar = 5.0 mm). 75, *A. albovestitus* (18 mi. SW Mendota, California); 76, *A. albovestitus* (16 mi. S. Vidal, California); 77, *A. albovestitus* (Virgin, Utah); 78, *A. albovestitus* (Phoenix, Arizona); 79, *A. albovestitus* (Yuma, Arizona); 80, *A. saginatus*.
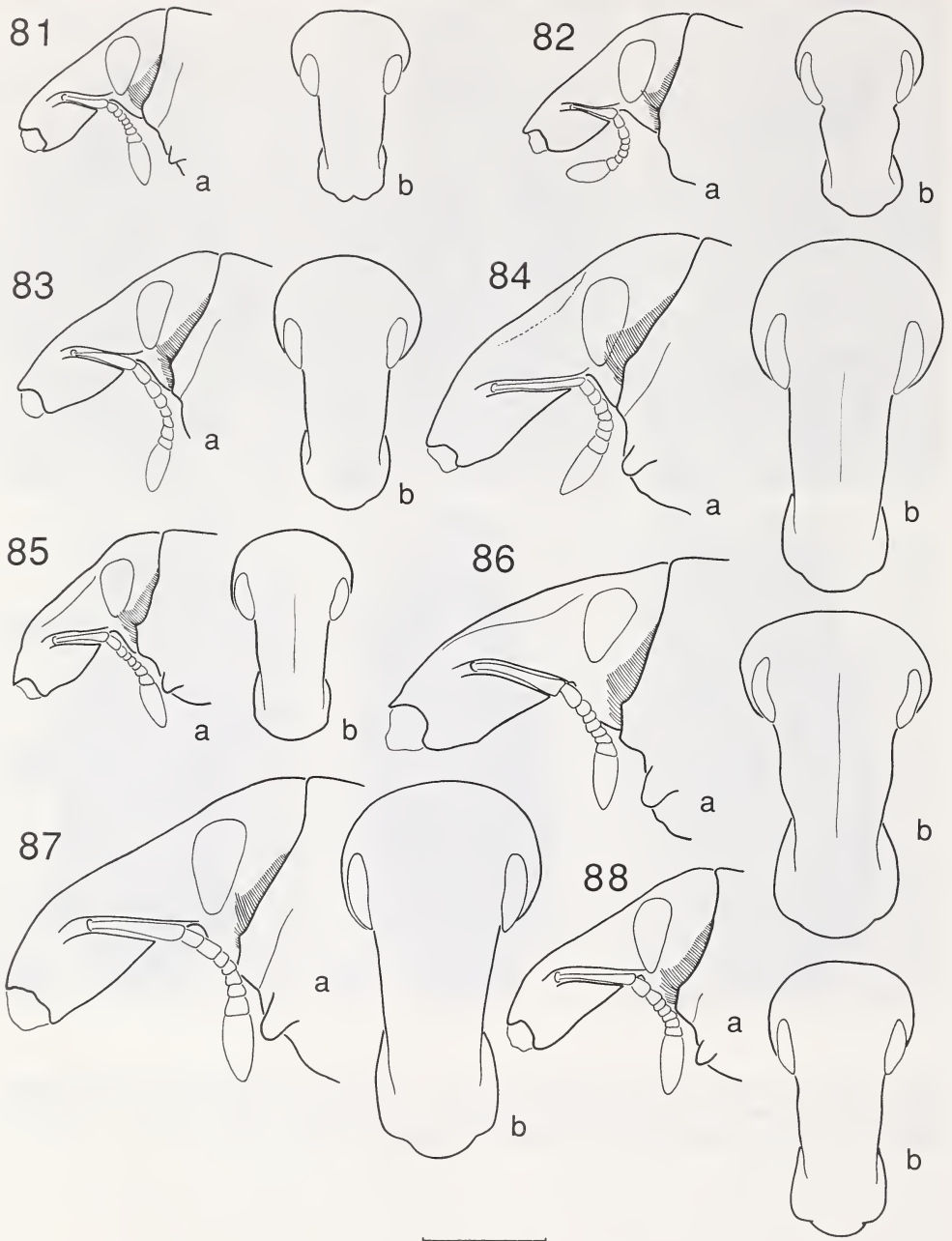
Figures 81–88. Head of *Apleurus* species (Scale bar = 2.4 mm) – a and b, lateral and dorsal views, respectively. 81, *A. hystrix*; 82, *A. aztecus*; 83, *A. lutulentus*; 84, *A. porosus*; 85, *A. angularis*; 86, *A. jacobinus*; 87, *A. saginatus*; 88, *A. albovestitus*.
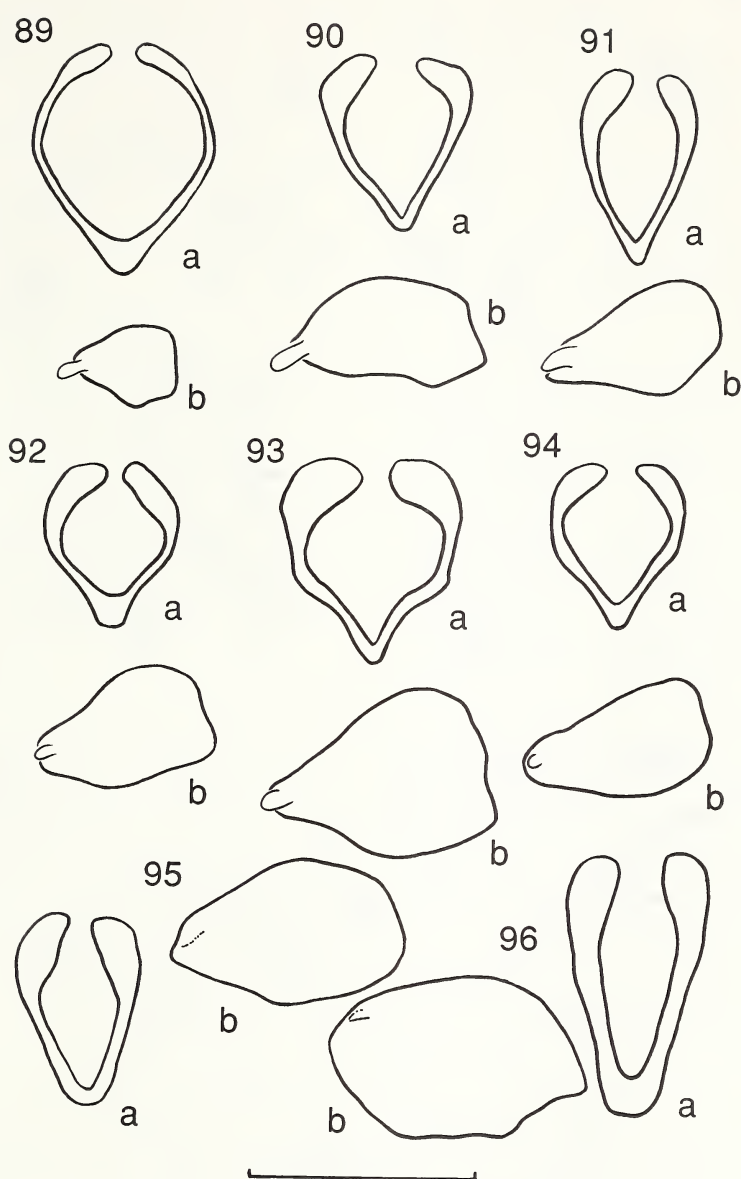
Figures 89–96. Female genitalia of *Apleurus* species. 89, *A. hystrix* (Scale bar = 1.0 mm); a, ventral view of sternum VIII; b, lateral view of gonocoxite II and stylus. 90, *A. aztecus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 91, *A. lutulentus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 92, *A. porosus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 93, *A. angularis*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 94, *A. jacobinus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 95, *A. albovestitus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 96, *A. saginatus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm).
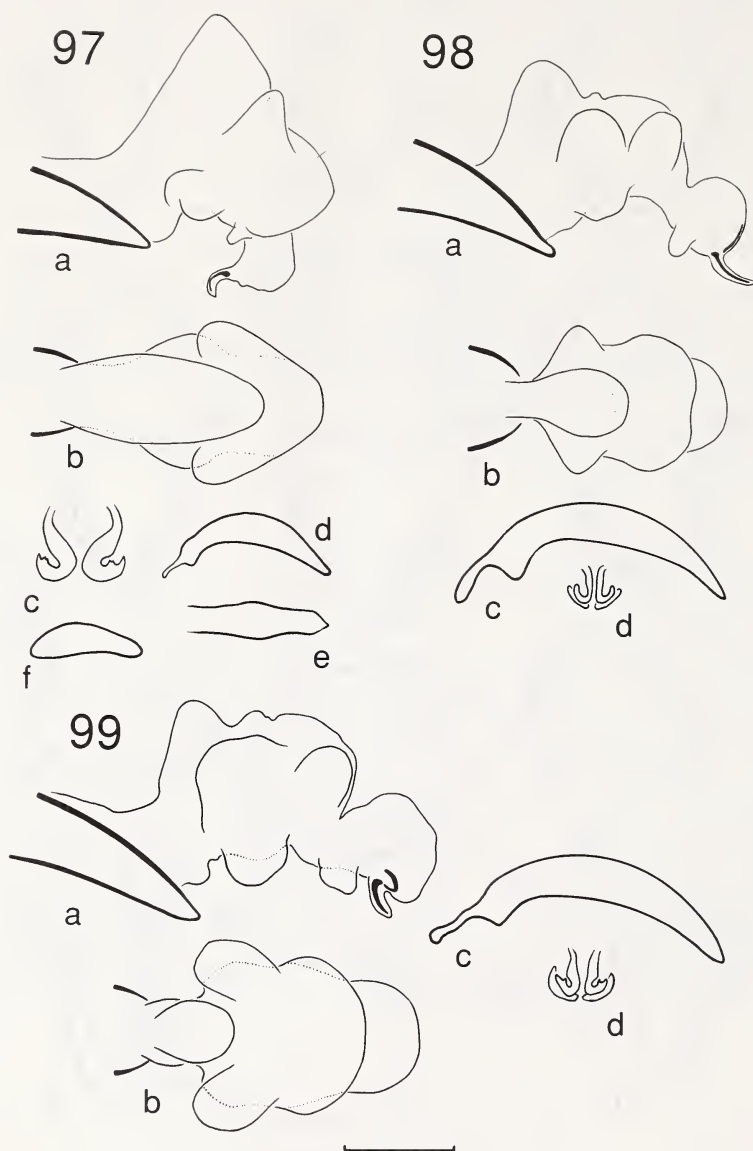
Figures 97–99. Male genitalia of *Apleurus* species. 97, *A. hystrix*; a, lateral view of internal sac (Scale bar = 0.4 mm); b, dorsal view of internal sac (Scale bar = 0.4 mm); c, ventral view of apical sclerite complex of internal sac (Scale bar = 0.3 mm); d, lateral view of aedeagus (Scale bar = 1.3 mm); e, ventral view of aedeagus (Scale bar = 1.3 mm); f, ventral view of sternite of sternum VII (Scale bar = 1.3 mm). 98, *A. aztecus*; a, lateral view of internal sac (Scale bar = 0.7 mm); b, dorsal view of internal sac (Scale bar = 0.7 mm); c, lateral view of aedeagus (Scale bar = 1.3 mm); d, ventral view of apical sclerite complex of internal sac (Scale bar = 0.6 mm). 99, *A. lutulentus* (Scale bars as in Fig. 98); a, lateral view of internal sac; b, dorsal view of internal sac; c, lateral view of aedeagus; d, ventral view of apical sclerite complex of internal sac.
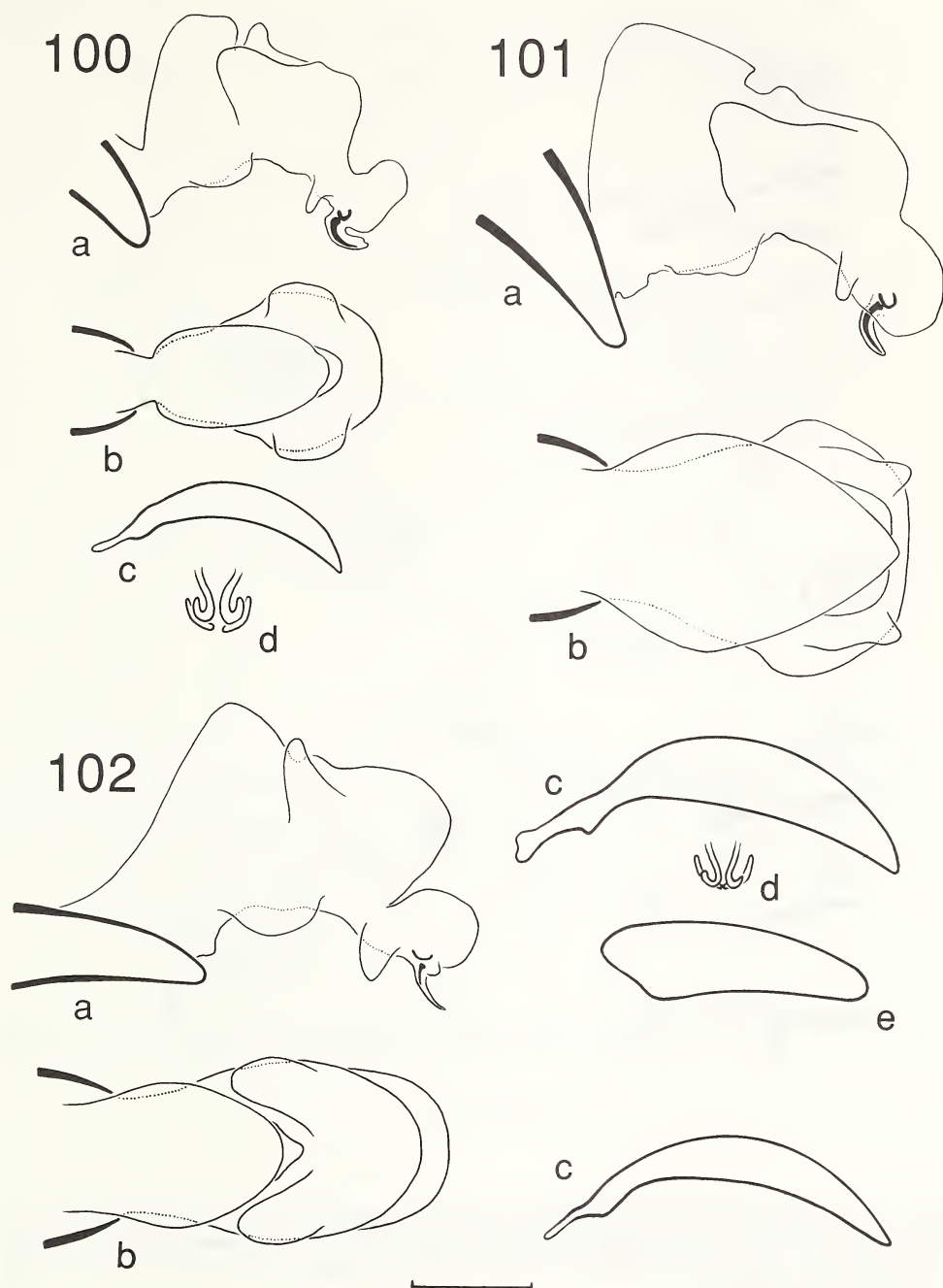
Figures 100–102. Male genitalia of *Apleurus* species – a, lateral view of internal sac (Scale bar = 0.7 mm); b, dorsal view of internal sac (Scale bar = 0.7 mm); c, lateral view of aedeagus (Scale bar = 1.3 mm); d, ventral view of apical sclerite complex of internal sac (Scale bar = 0.6 mm); e, ventral view of sternite of sternum VII. 100, *A. angularis*; 101, *A. jacobinus*; 102, *A. porosus*.
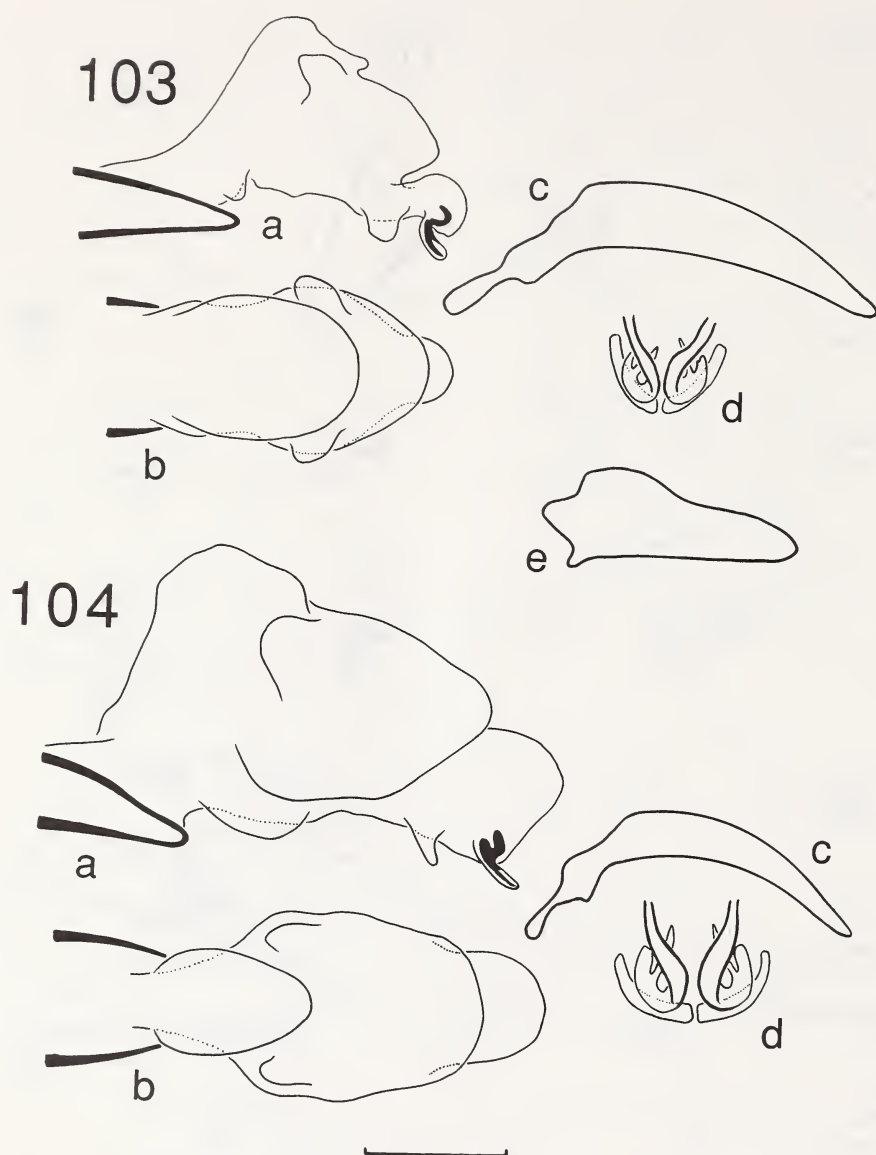
Figures 103–104. Male genitalia of *Apleurus* species – a, lateral view of internal sac (Scale bar = 0.7 mm); b, dorsal view of internal sac (Scale bar = 0.7 mm); c, lateral view of aedeagus (Scale bar = 1.3 mm); d, ventral view of apical sclerite complex of internal sac (Scale bar = 0.6 mm); e, ventral view of sternite of sternum VII (Scale bar = 1.3 mm). 103, *A. albovestitus*; 104, *A. saginatus*.
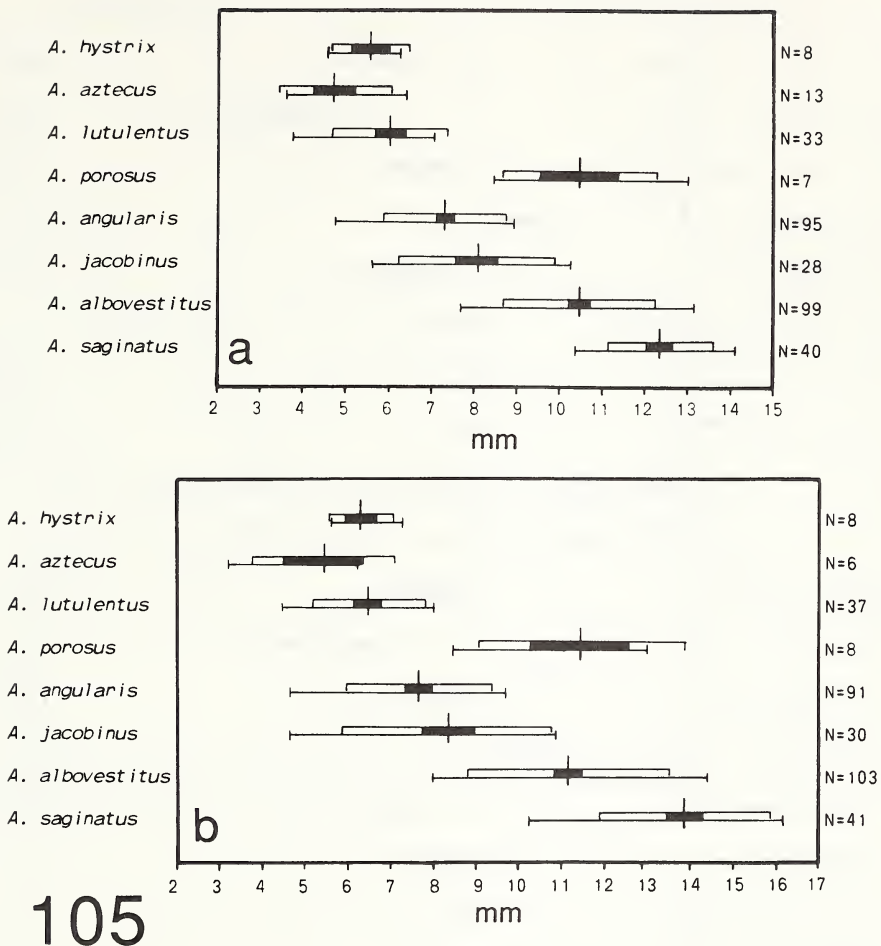
Figure 105. Hubbs-Hubbs diagram illustrating variation among specimens of *Apleurus* species: length of elytra (LEl) – a, males; b, females. See caption for Fig. 49 for explanation.
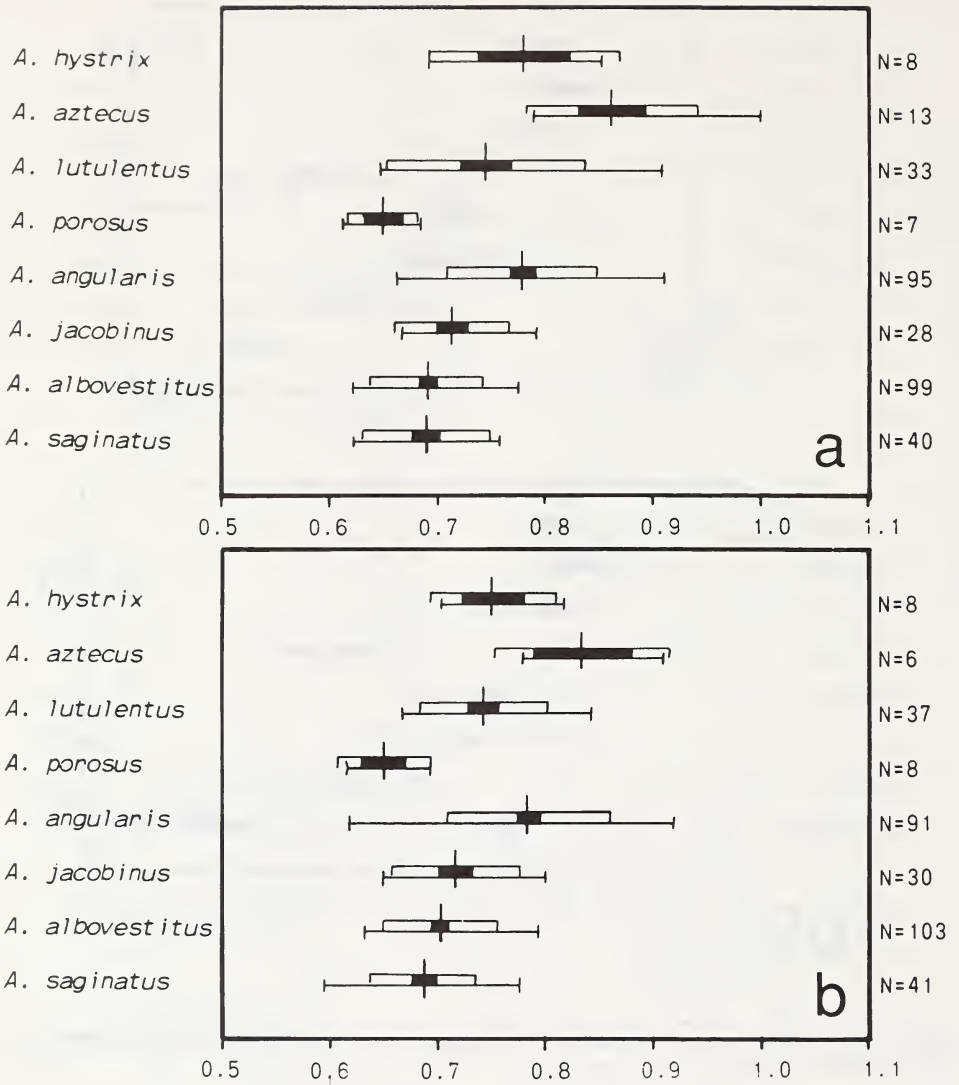
Figure 106. Hubbs-Hubbs diagram illustrating variation among specimens of *Apleurus* species: form of rostrum (WRA/LR) – a, males; b, females. See caption for Fig. 49 for explanation.
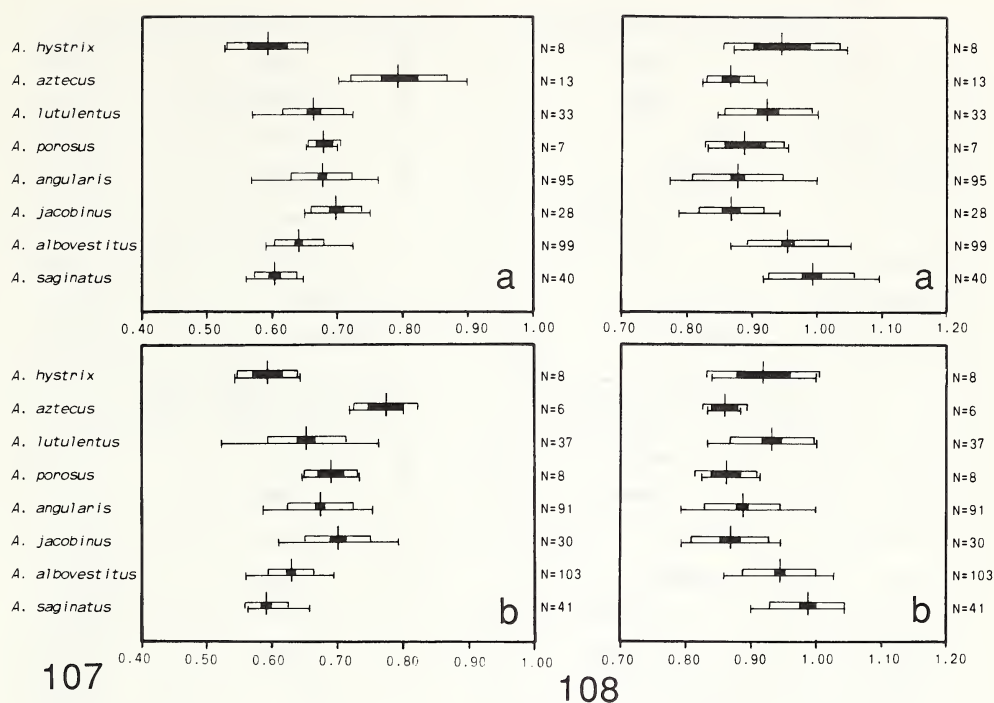
Figures 107–108. Hubbs-Hubbs diagrams illustrating variation among specimens of *Apleurus* species – a, males; b, females. See caption for Fig. 49 for explanation. 107, form of elytra (WElM/LEl); 108, width of frons compared to width at apex of rostrum (WRA/WF).
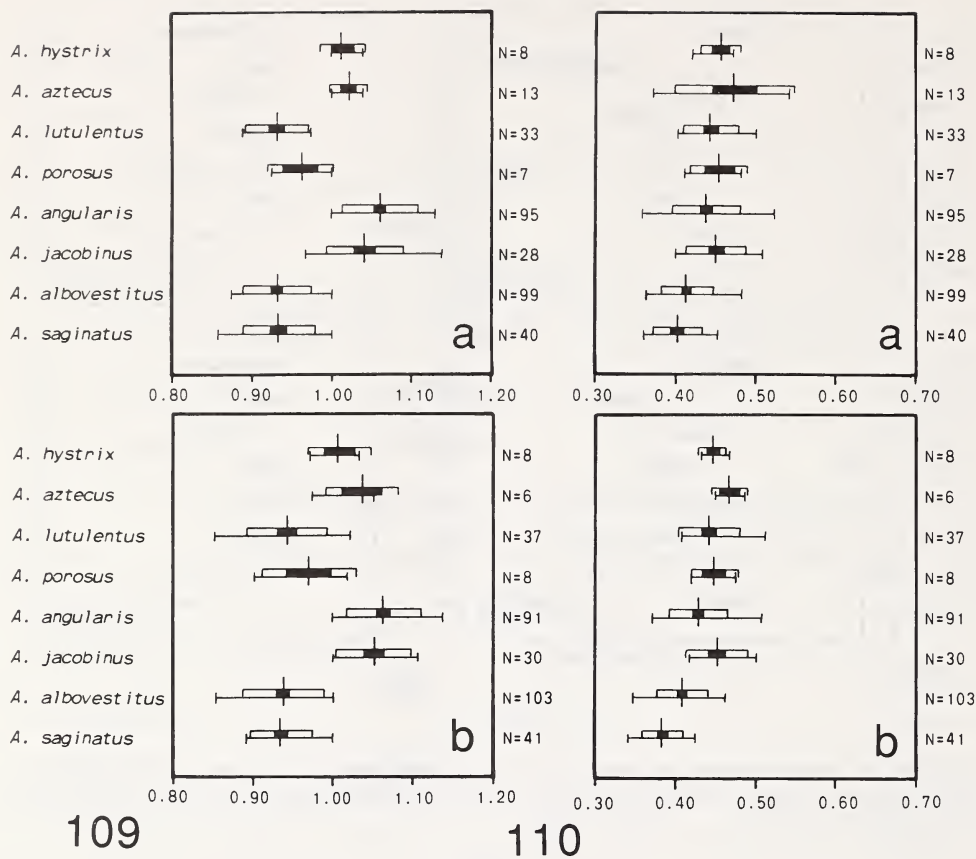
Figures 109–110: Hubbs-Hubbs diagrams illustrating variation among specimens of *Apleurus* species – a, males; b, females. See caption for Fig. 49 for explanation. 109, form of pronotum (WPT/WPB); 110, length of pronotum compared to length elytra (LP/LEl).
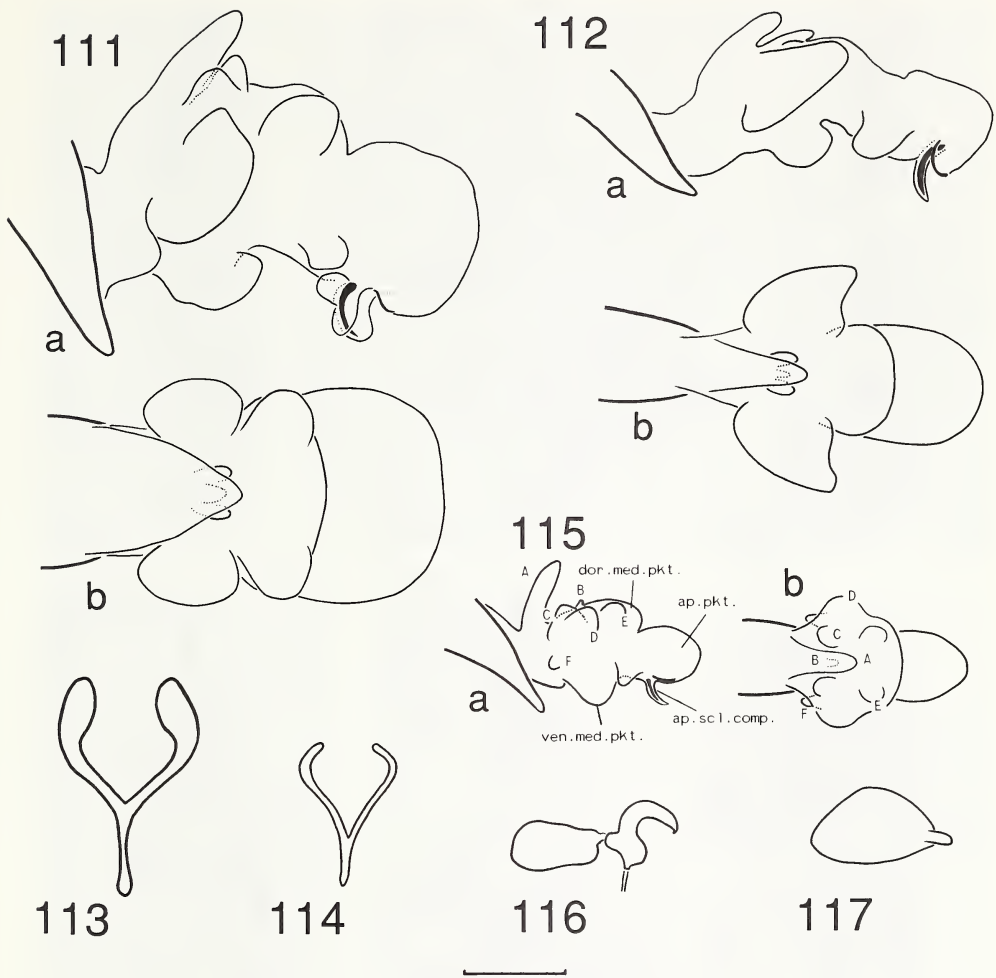
Figures 111–117. 111, Male genitalia of *Cylindropterus luxeri* (Scale bar = 0.7 mm); a, lateral view of internal sac; b, dorsal view of internal sac. 112, Male genitalia of *Lixus (Lixoglyptus) spartii* (Scale bar = 0.7 mm); a, lateral view of internal sac; b, dorsal view of internal sac. 113, Ventral view of sternum VIII of female *Cylindropterus luxeri* (Scale bar = 1.3 mm). 114, Ventral view of sternum VIII of female *Lixus (Lixoglyptus) spartii* (Scale bar = 1.3 mm). 115, Internal sac of male *Cleonidius* Lobes and pockets of internal sac labelled as noted (Scale bar = 0.7 mm); a, lateral view; b, dorsal view. 116, Spermatheca of female *Cleonidius* (Scale bar = 0.3 mm). 117, Lateral view of gonocoxite II and stylus of *Cleonidius* (Scale bar = 0.7 mm).
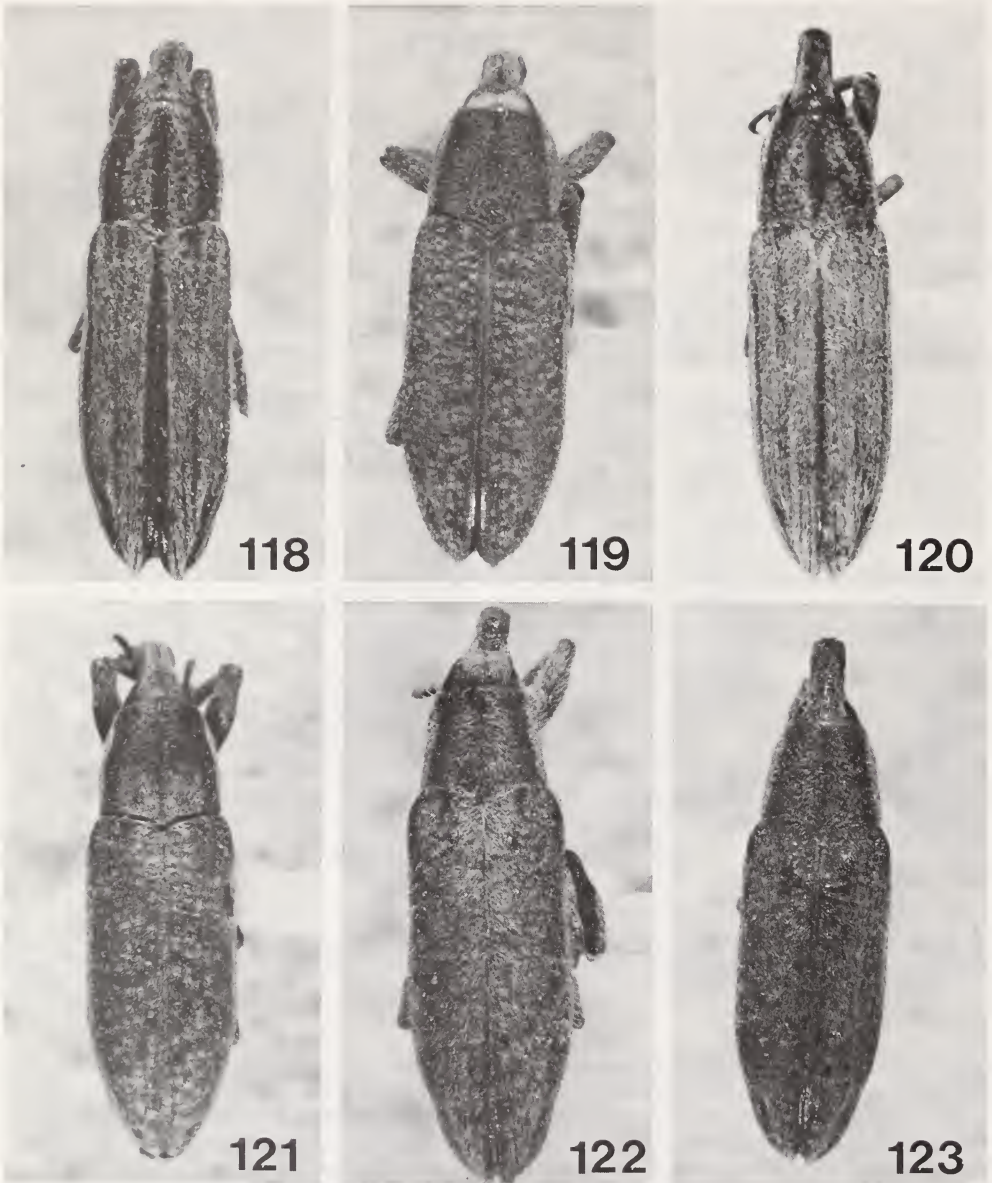
Figures 118–123. Dorsal habitus of: 118, *Cleonidius erysimi* (Scale bar = 4.0 mm); 119, *C. eustictorrhinus* (Scale bar = 4.0 mm); 120, *C. pleuralis* (Scale bar = 4.0 mm); 121, *C. subcylindricus* (Scale bar = 4.0 mm); 122, *C. longinasus* (Scale bar = 4.0 mm); 123, *C. texanus* (Scale bar = 4.0 mm).
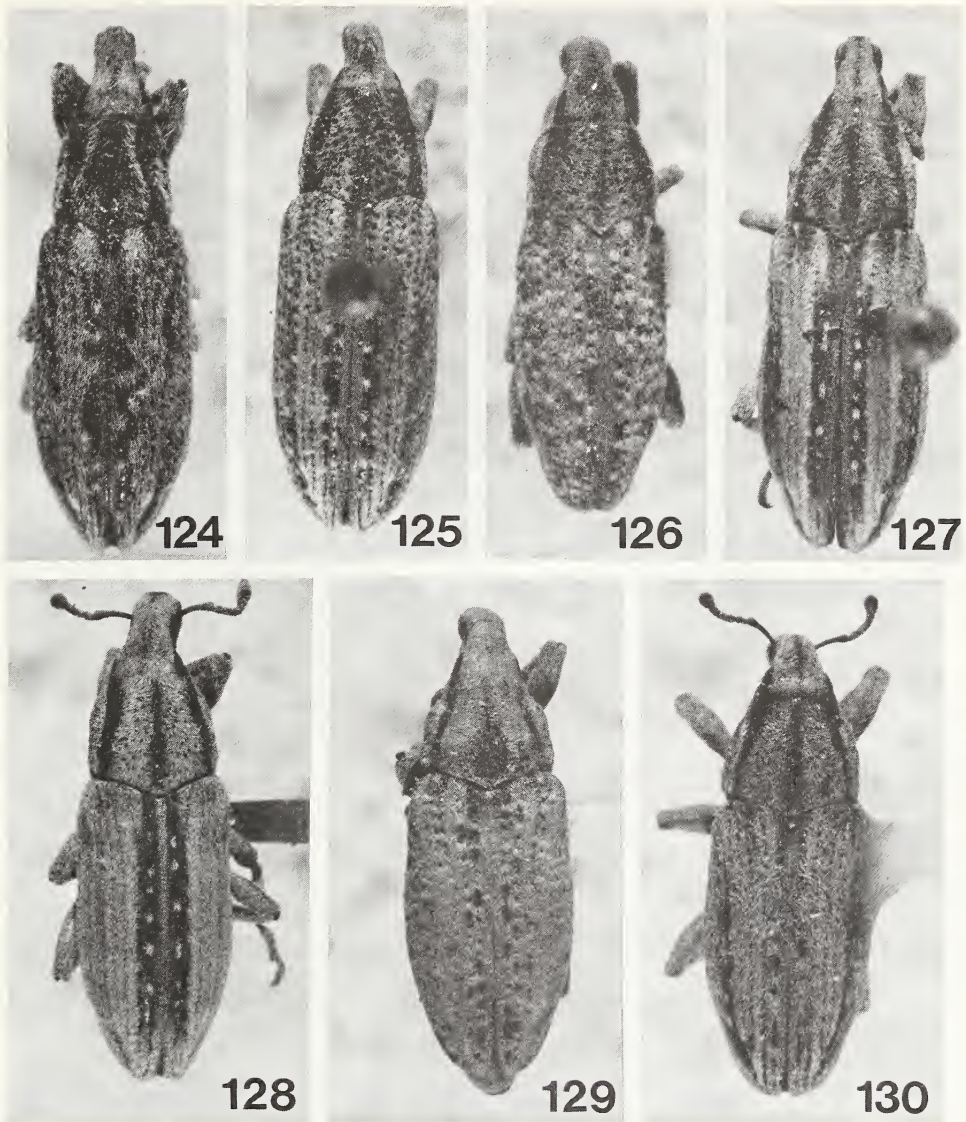
Figures 124–130. Dorsal habitus of: 124, *Cleonidius americanus* 125, *C. frontalis* (Scale bar = 4.0 mm); 126, *C. canescens* (Scale bar = 4.0 mm); 127, *C. infrequens* (Scale bar = 4.0 mm); 128, *C. puberulus* (Scale bar = 4.0 mm); 129, *C. collaris* (Scale bar = 4.0 mm); 130, *C. notolomus*. (Scale bar = 4.0 mm).
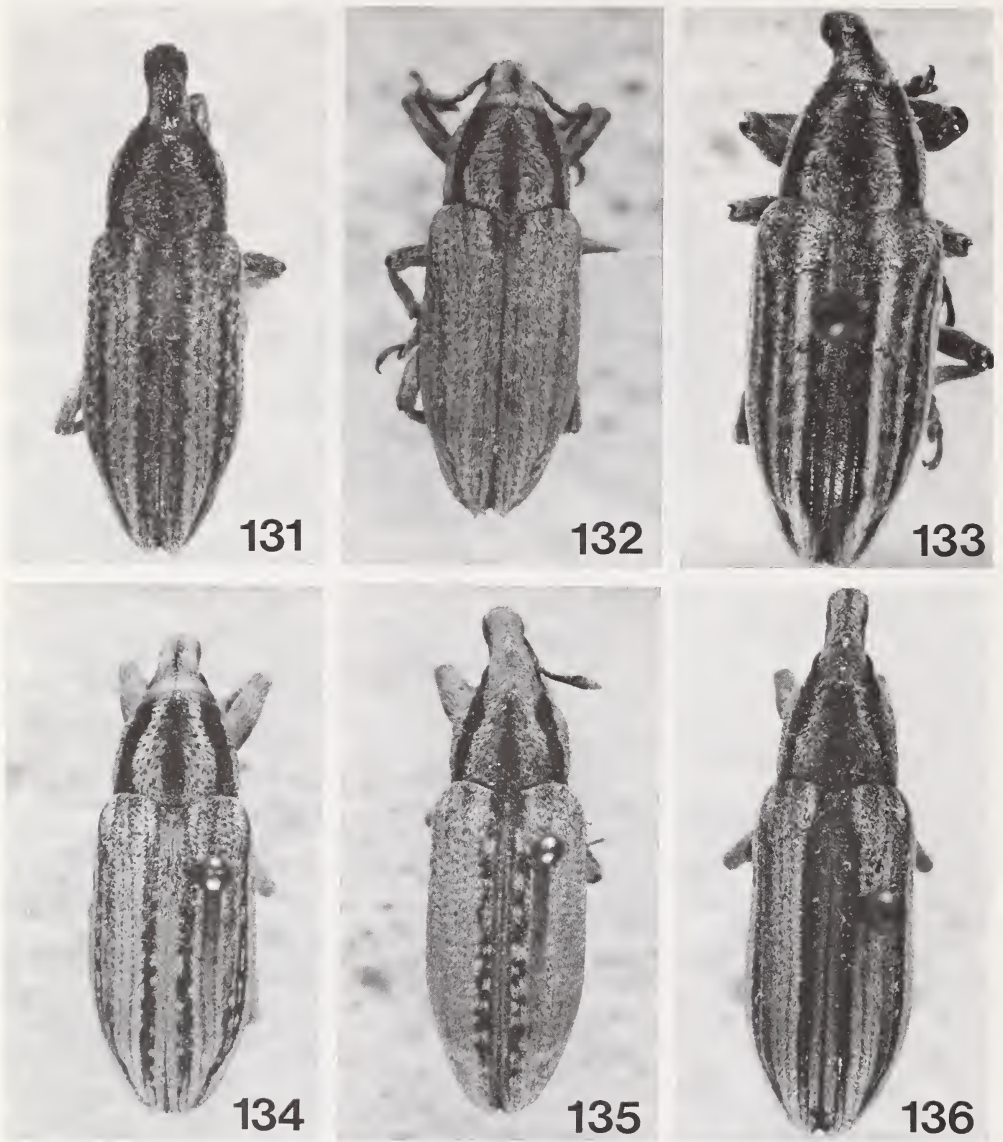
Figures 131–136. Dorsal habitus of: 131, *Cleonidius poricollis* (Scale bar = 4.0 mm); 132, *C. calandroides* (Scale bar = 4.0 mm); 133, *C. boucardi* (Scale bar = 5.0 mm); 134, *C. trivittatus* (Scale bar = 5.0 mm); 135, *C. placidus* (Scale bar = 5.0 mm); 136, *C. quadrilineatus* (Scale bar = 4.0 mm).
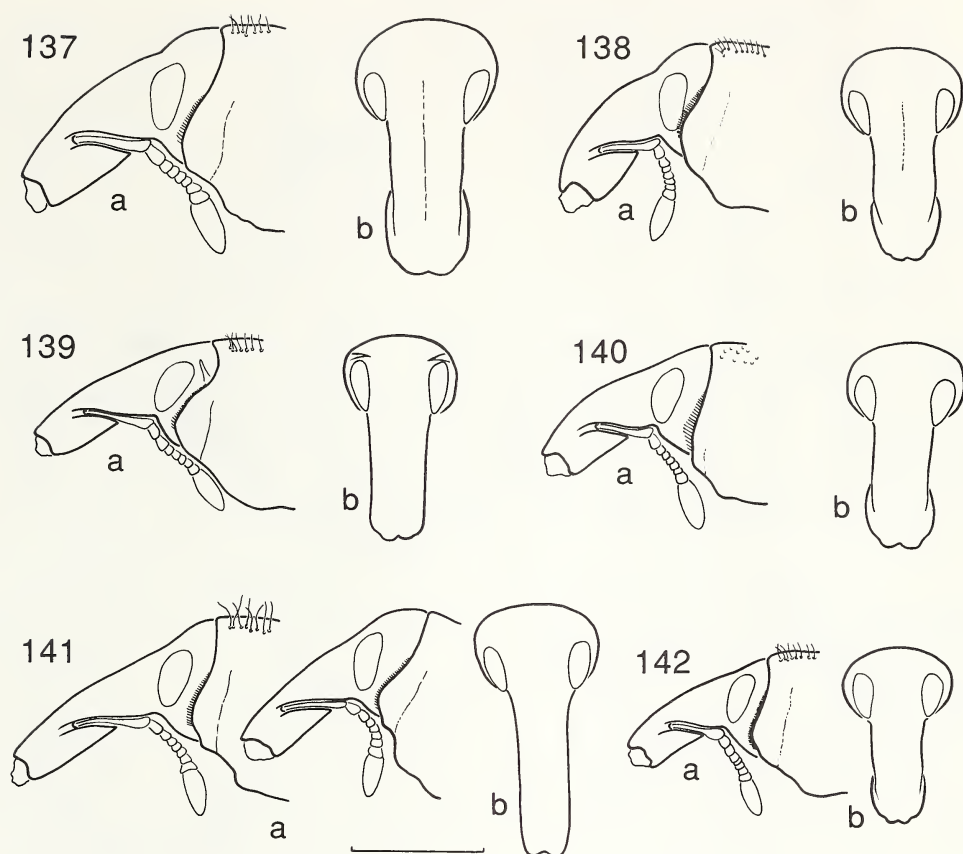
Figures 137–142. Head of *Cleonidius* species (Scale bar = 2.3 mm) – a and b, lateral and dorsal view, respectively. 137, *Cleonidius erysimi*; 138, *C. eustictorrhinus*; 139, *C. pleuralis*; 140, *C. subcylindricus*; 141, *C. longinasus*; a, Lateral view of heads of male and female; b, Dorsal view of head of female; 142, *Cleonidius texanus*.
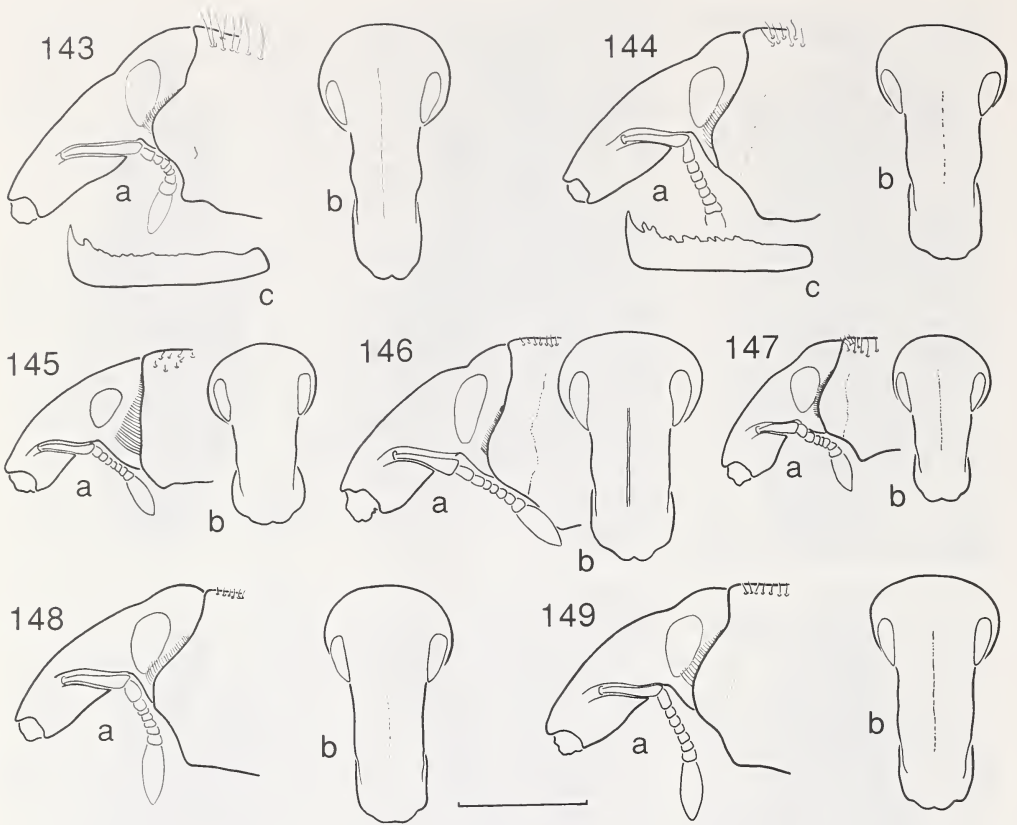
Figures 143–149. Head and femur of *Cleonidius* species – (Scale bar = 2.3 mm) a and b, lateral and dorsal view of head, respectively; c, lateral view of pro-tibia of female. 143, *C. americanus*; 144, *C. frontalis*; 145, *C. canescens*; 146, *C. infrequens*; 147, *C. puberulus*; 148, *C. collaris*; 149, *C. notolomus*.
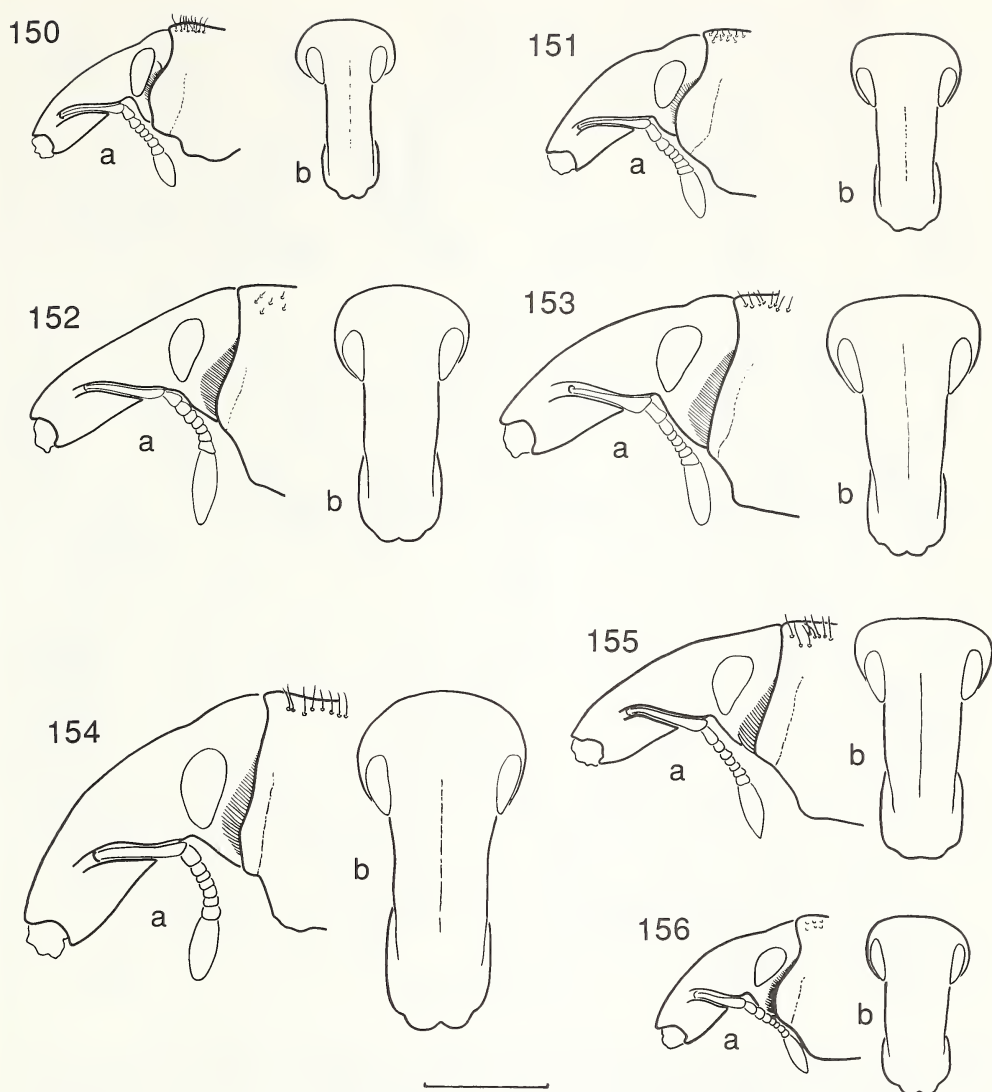
Figures 150–156. Head of *Cleonidius* species (Scale bar = 2.3 mm) – a and b, lateral and dorsal vies, respectively. 150, *C. poricollis*; 151, *C. calandroides*; 152, *C. boucardi*; 153, *C. trivittatus*; 154, *C. placidus*; 155, *C. quadrilineatus*; 156, *C. vibex*. (Scale bar = 2.3 mm).
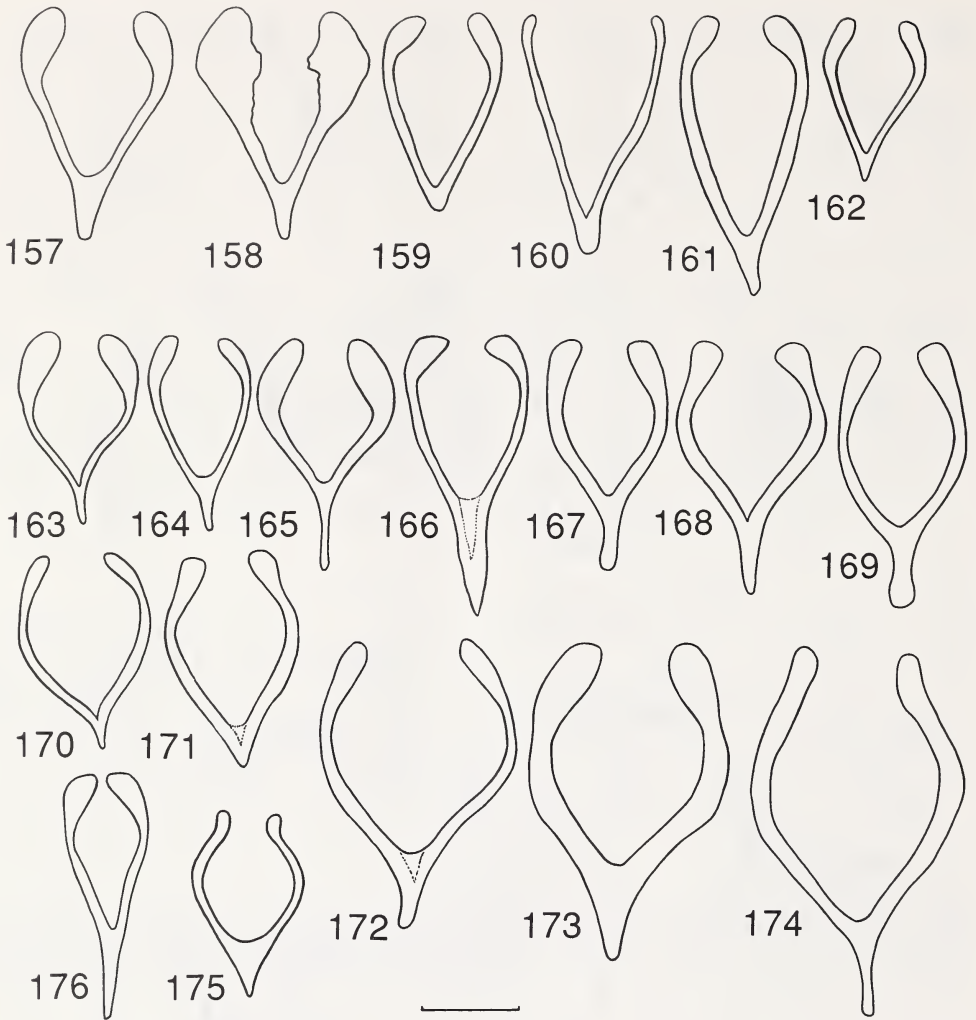
Figures 157–176. Ventral view of sternum VIII of female *Cleonidius* species (Scale bar = 0.8 mm). 157, *C. erysimi*; 158, *C. eustictorrhinus*; 159, *C. pleuralis*; 160, *C. subcylindricus*; 161, *C. longinasus*; 162, *C. texanus*; 163, *C. americanus*; 164, *C. frontalis*; 165, *C. canescens*; 166, *C. infrequens*; 167, *C. puberulus*; 168, *C. notolomus*; 169, *C. collaris*; 170, *C. poricollis*; 171, *C. calandroides*; 172, *C. boucardi*; 173, *C. trivittatus*; 174, *C. placidus*; 175, *C. quadrilineatus*; 176, *C. vibex*. (Scale bar = 0.8 mm).
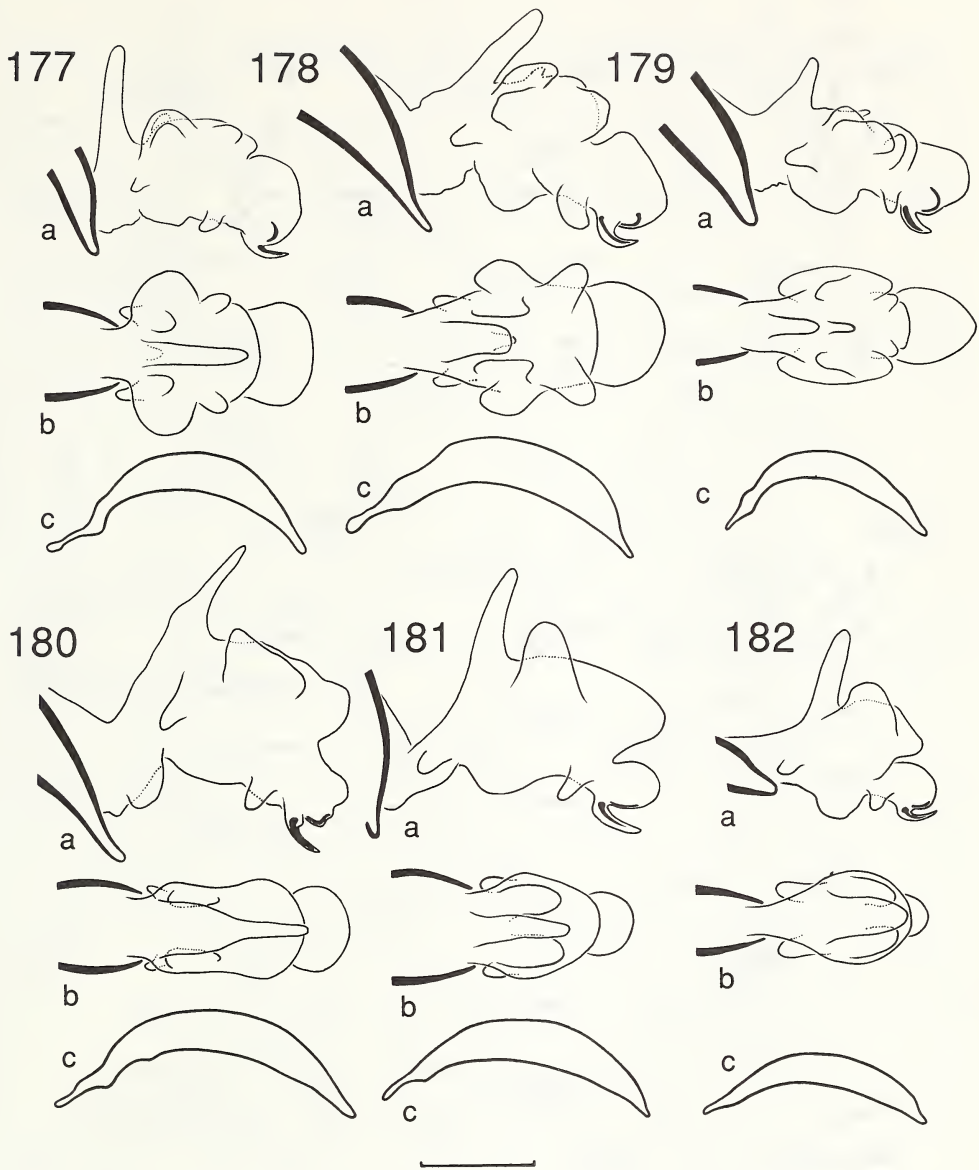
Figures 177–182. Male genitalia of *Cleonidius* species – a and b, internal sac, lateral and dorsal view, respectively; c, lateral view of aedeagus (Scale bars, 0.7 mm, 0.7 mm and 1.3 mm respectively). 177, *C. erysimi*; 178, *C. eustictorrhinus*; 179, *C. pleuralis*; 180, *C. subcylindricus*; 181, *C. longinasus*; 182, *C. texanus*.
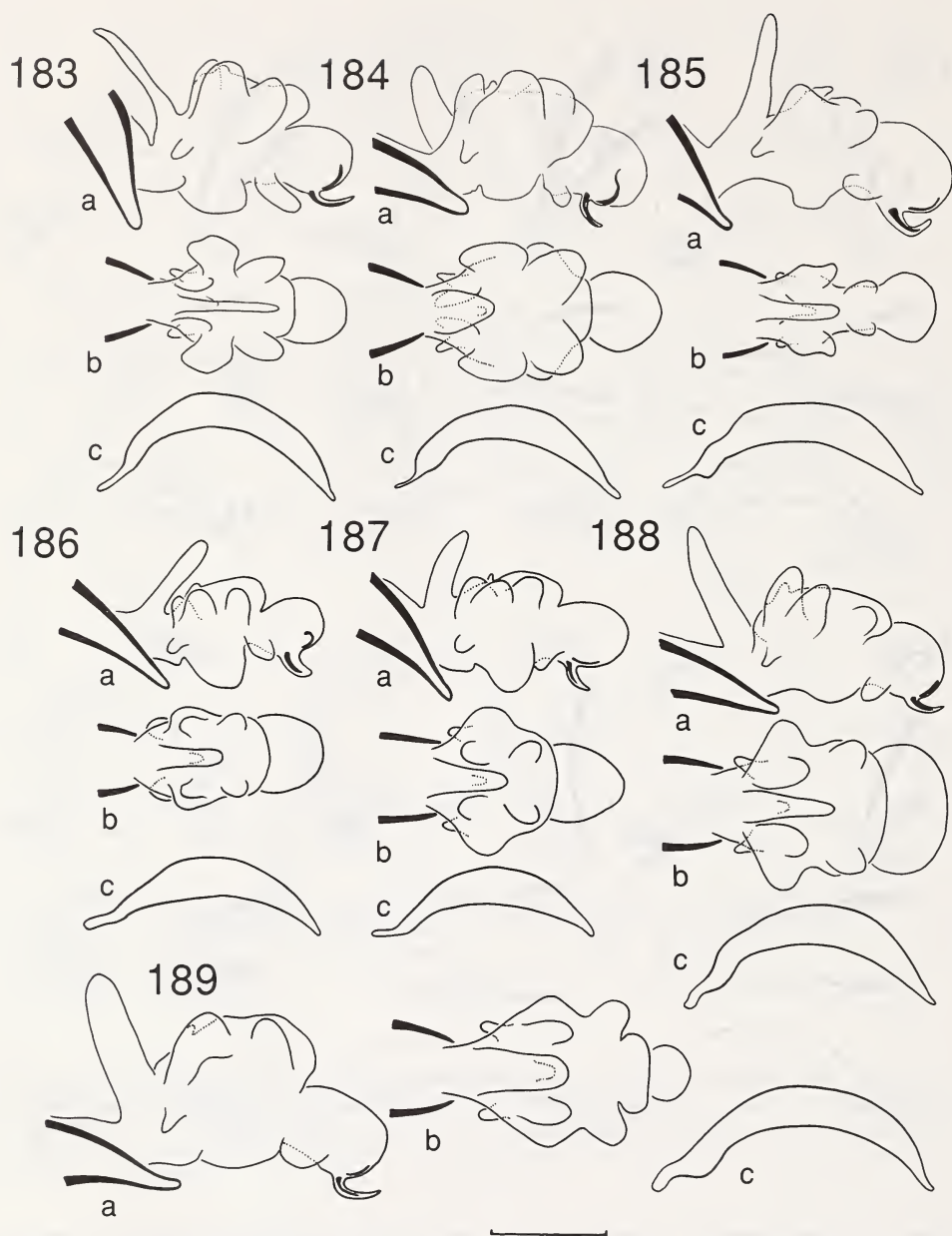
Figures 183–189. Male genitalia of *Cleonidius* species – a and b, internal sac, lateral and dorsal view, respectively; c, lateral view of aedeagus (Scale bars, 0.7 mm, 0.7 mm and 1.3 mm respectively). 183, *C. americanus*; 184. *C. frontalis*; 185, *C. canescens*; 186, *C. infrequens*; 187, *C. puberulus*; 188, *C. notolomus*; 189, *C. collaris*.
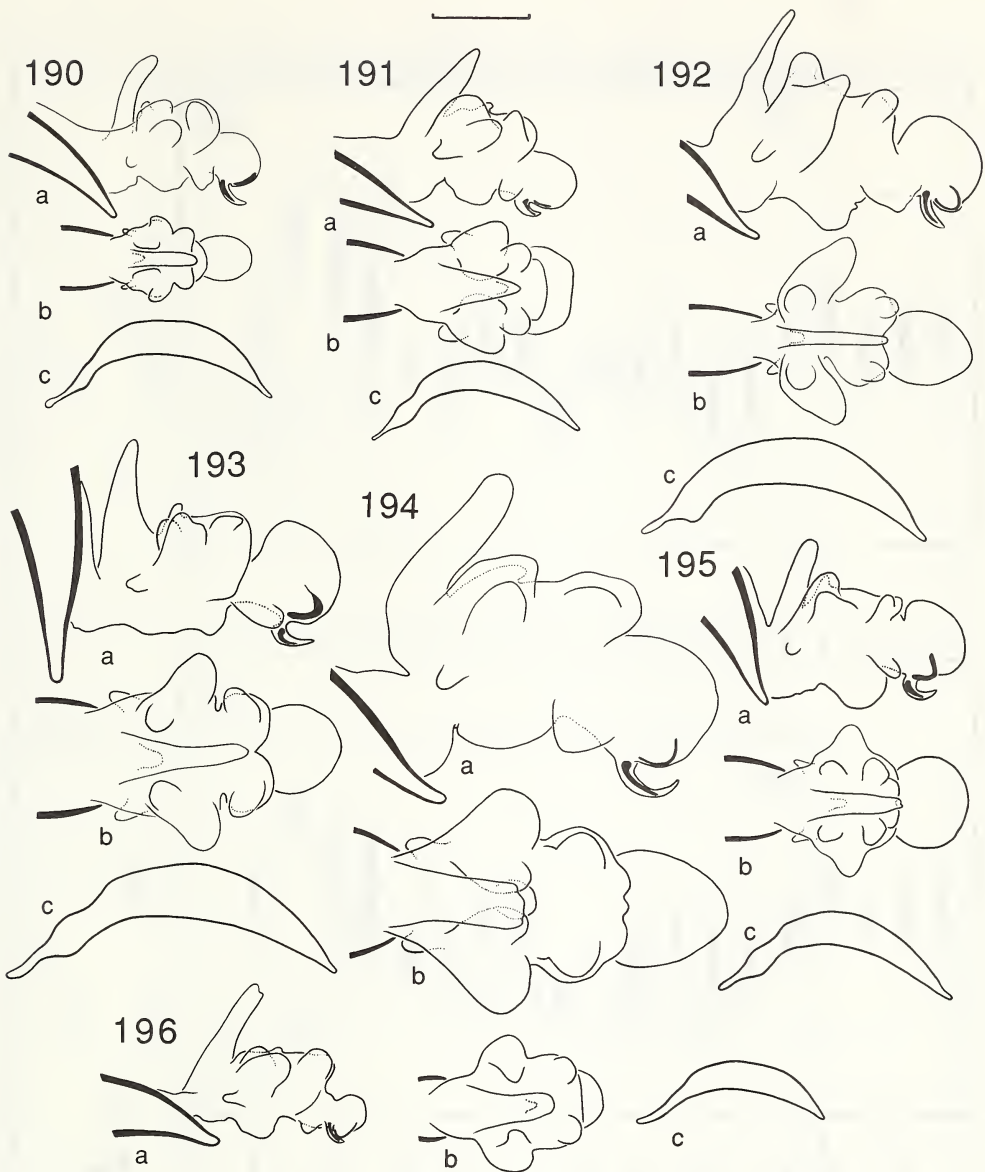
Figures 190–196. Male genitalia of *Cleonidius* species – a and b, internal sac, lateral and dorsal views, respectively; c, lateral view of adeagus (Scale bars, 0.7 mm, 0.7 mm and 1.3 mm, respectively): 190, *C. poricollis*; 191, *C. calandroides*; 192, *C. boucardi*; 193, *C. trivittatus*; 194, *C. placidus*; 195, *C. quadrilineatus*; 196, *C. vibex*.
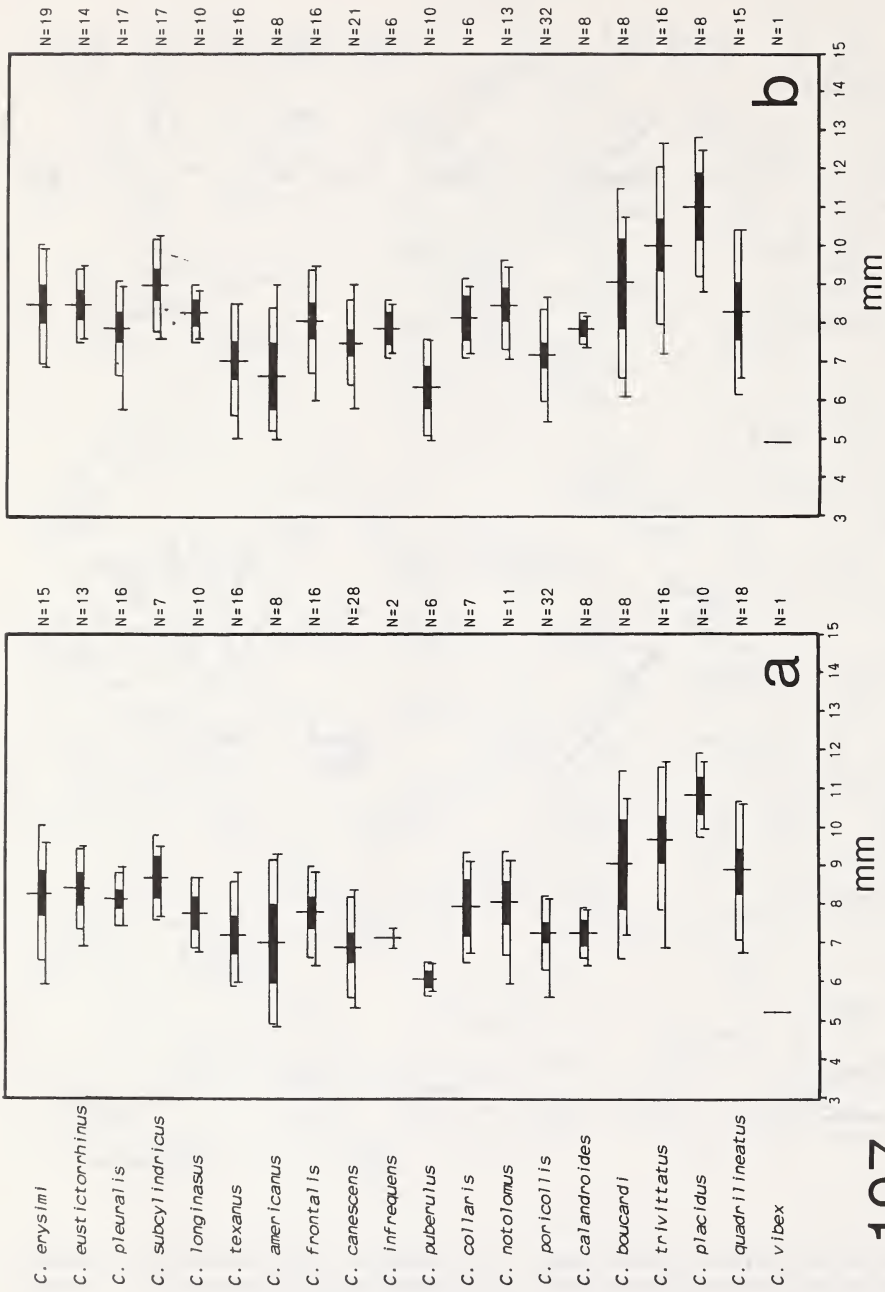
Figure 197. Hubbs-Hubbs diagram illustrating variation among specimens of *Cleonidius* species; length of elytra (LEl) – a, males; b, females. See caption for Fig. 49 for explanation.
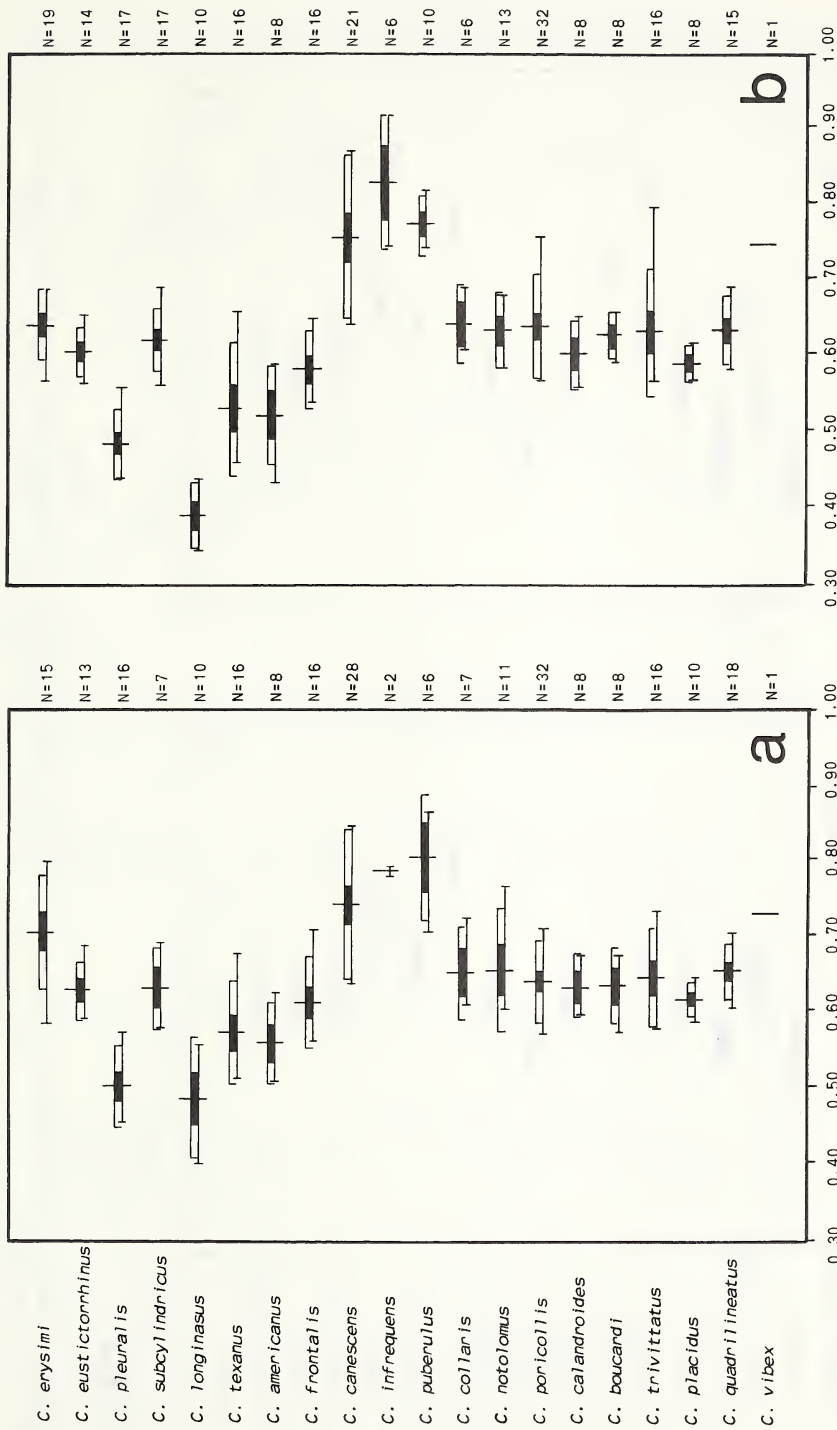
Figure 198. Hubbs-Hubbs diagram illustrating variation among specimens of *Cleonidius* species; form of rostrum (WRA/LR) – a, males; b, females. See caption for Fig. 49 for explanation.
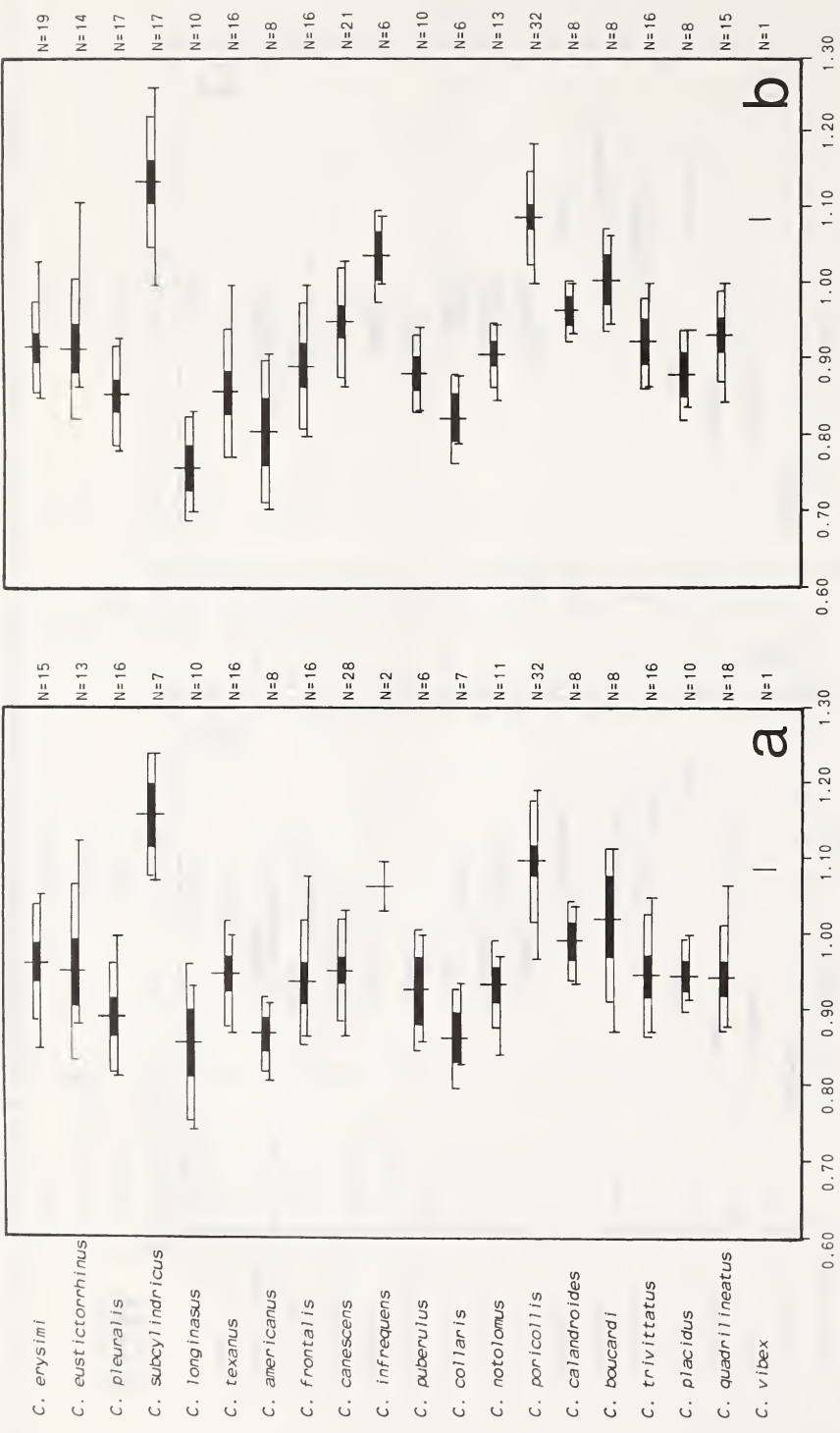
Figure 199. Hubbs-Hubbs diagram illustrating variation among specimens of *Cleonidius* species; width frons compared to width at apex of rostrum (WRA/WF) – a, males; b, females. See caption for Fig. 49 for explanation.
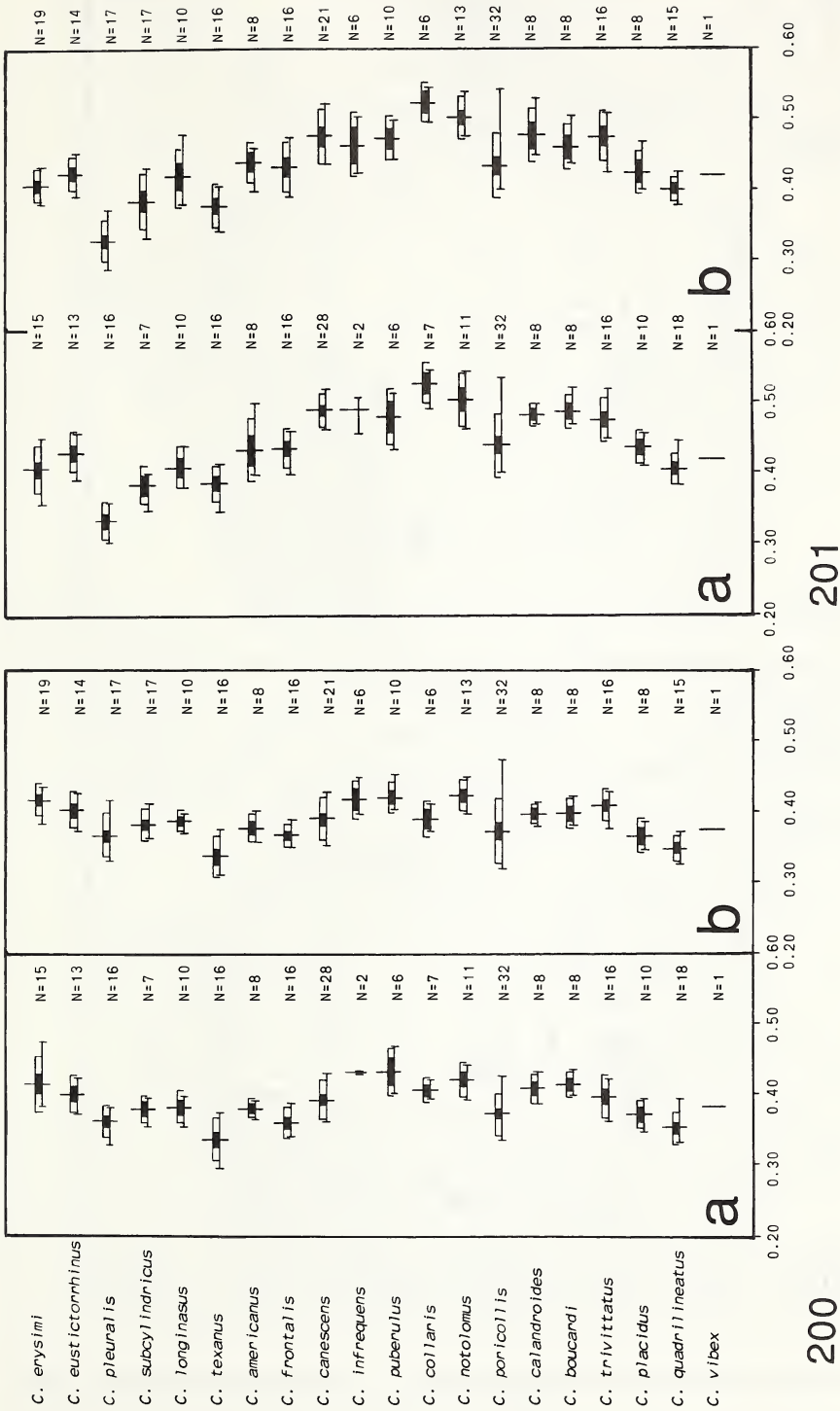
Figures 200–201. Hubbs-Hubbs diagrams illustrating variation among specimens of *Cleonidius* species – a, males; b, females. See caption for Fig. 49 for explanation. 200, length pronotum compared to length of elytra (LP/LEI); 201, form of elytra (WEIM/LEI).
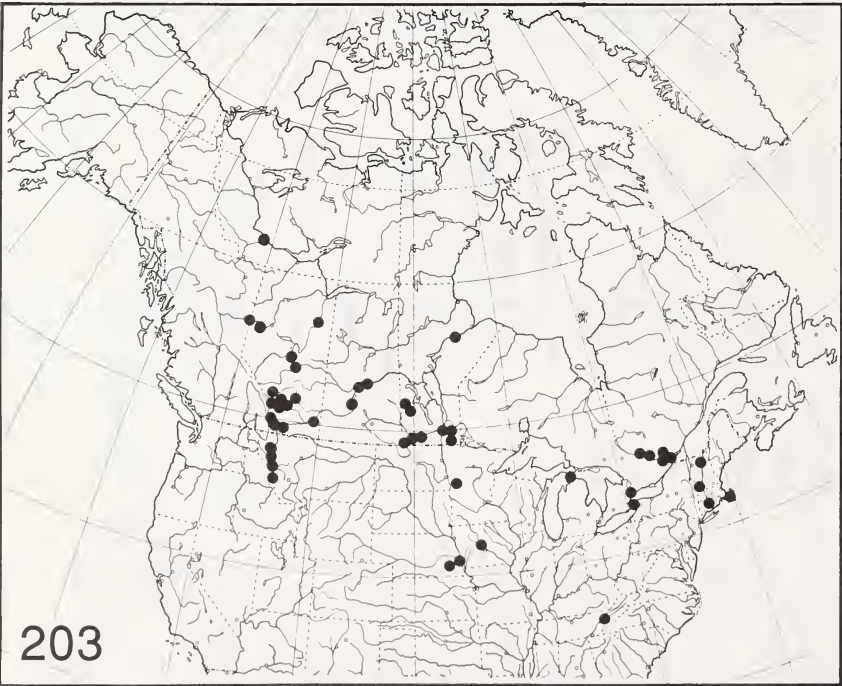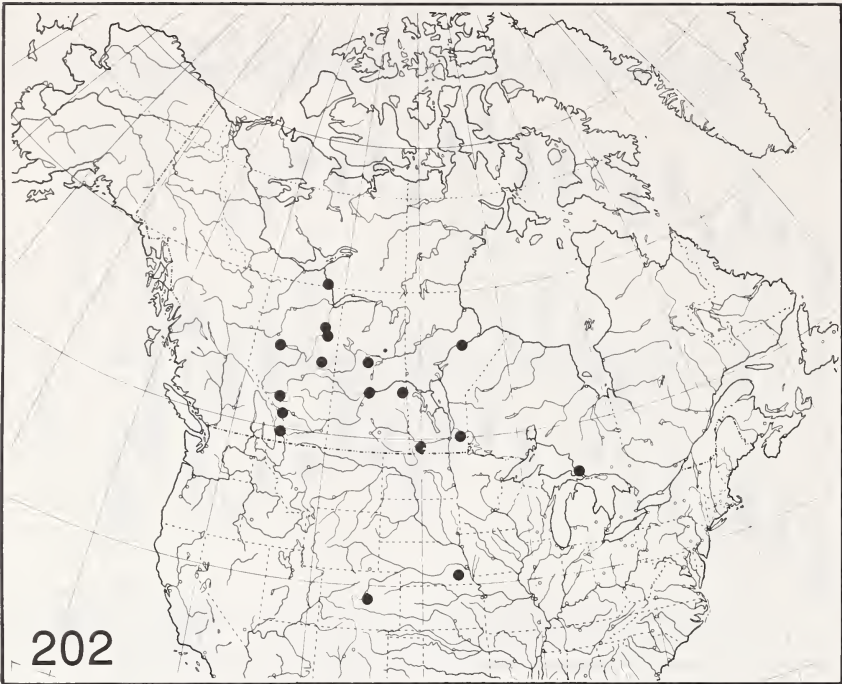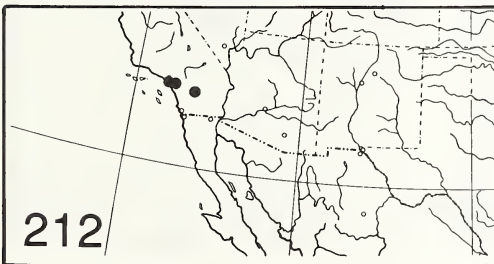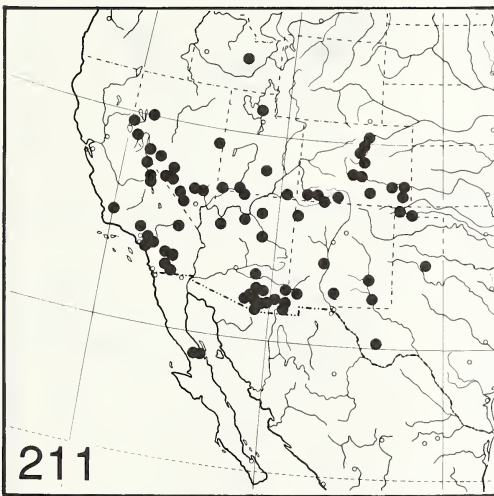
Figures 202–203. Maps illustrating position of collecting localities for: 202, *Stephanocleonus immaculatus*; 203, *S. parshus*.
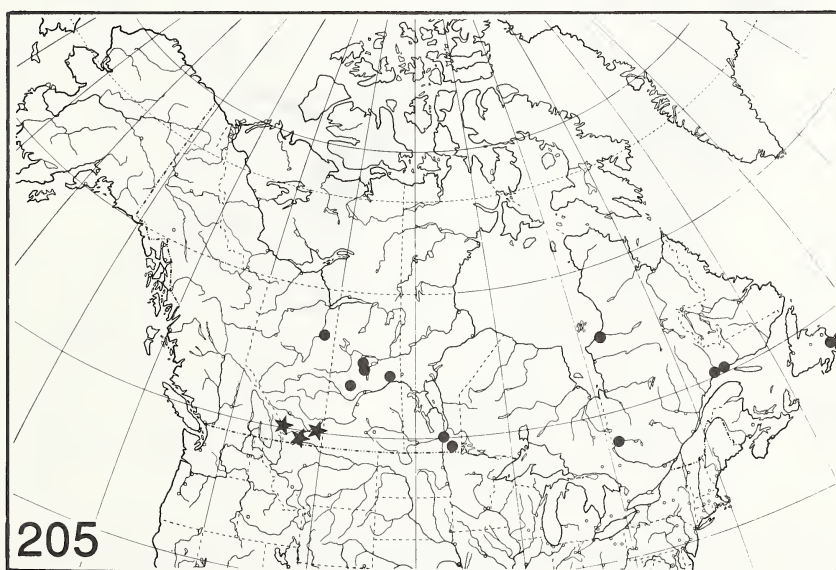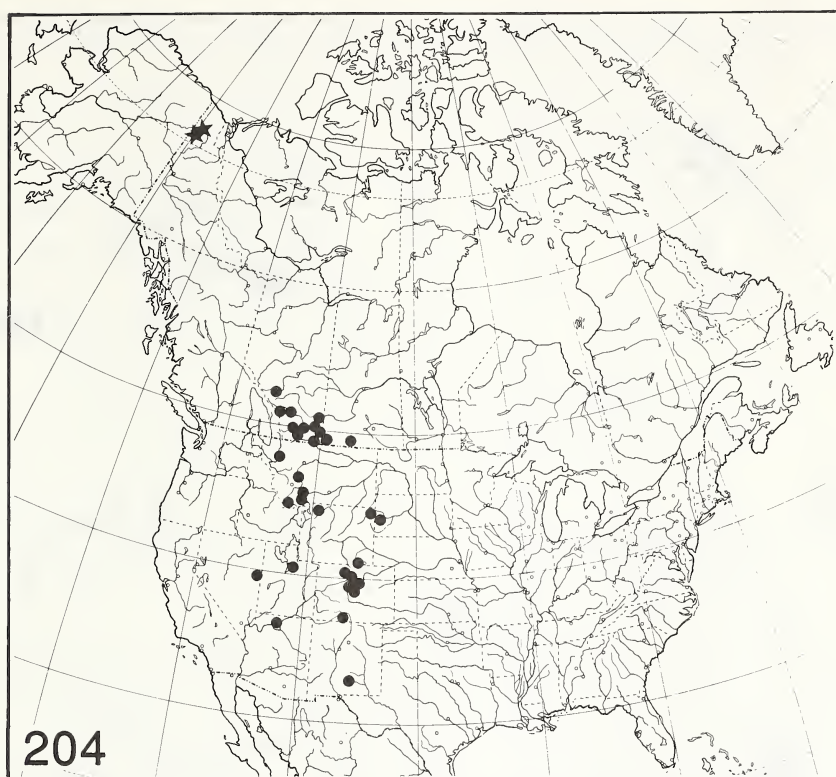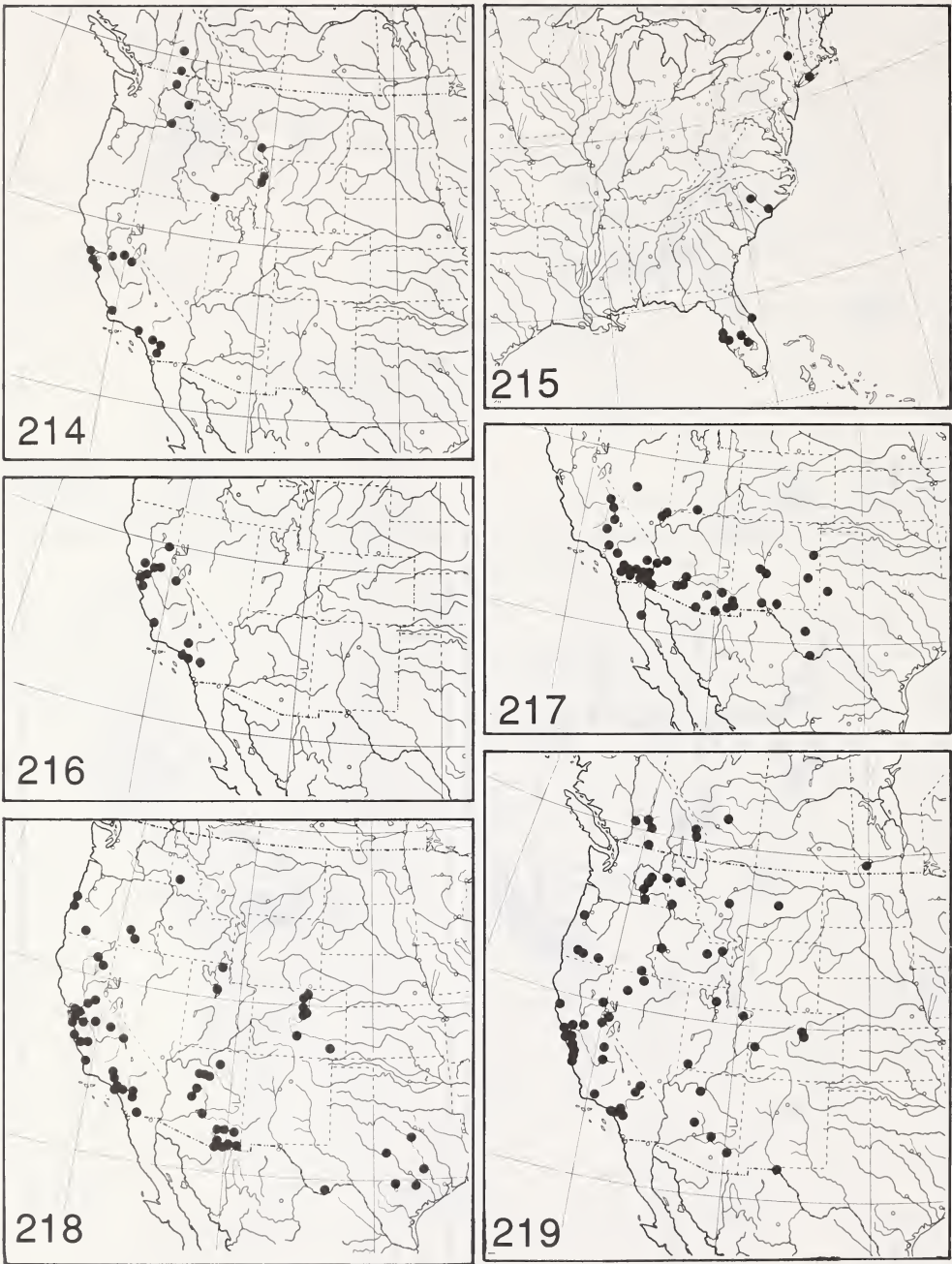
Figures 204–205. Maps illustrating position of collecting localities for: 204, *Stephanocleonus confusus* (dots) and *S. stenothorax* (stars); 205, *S. plumbeus* (dots) and *S. cristaticollis* (stars).
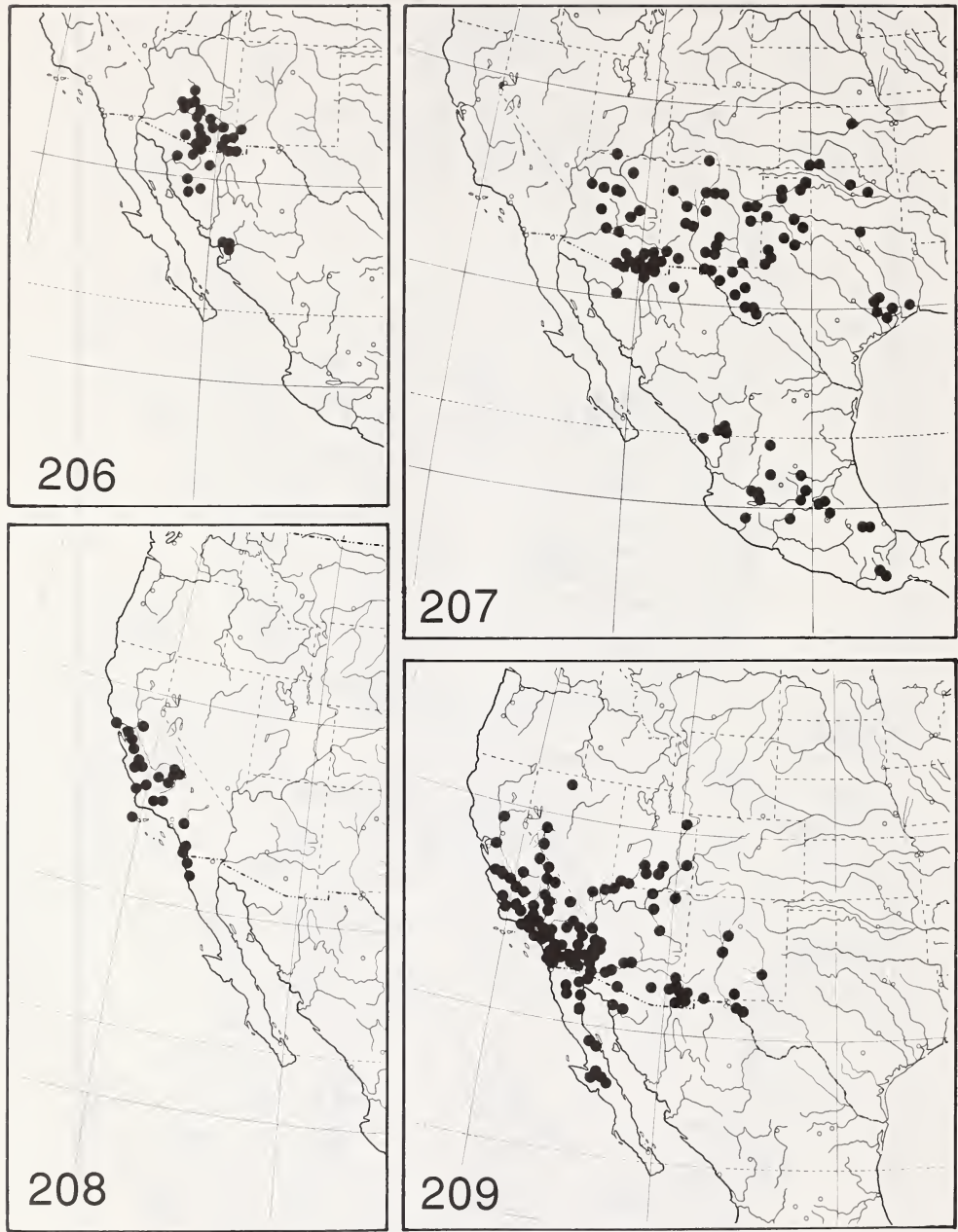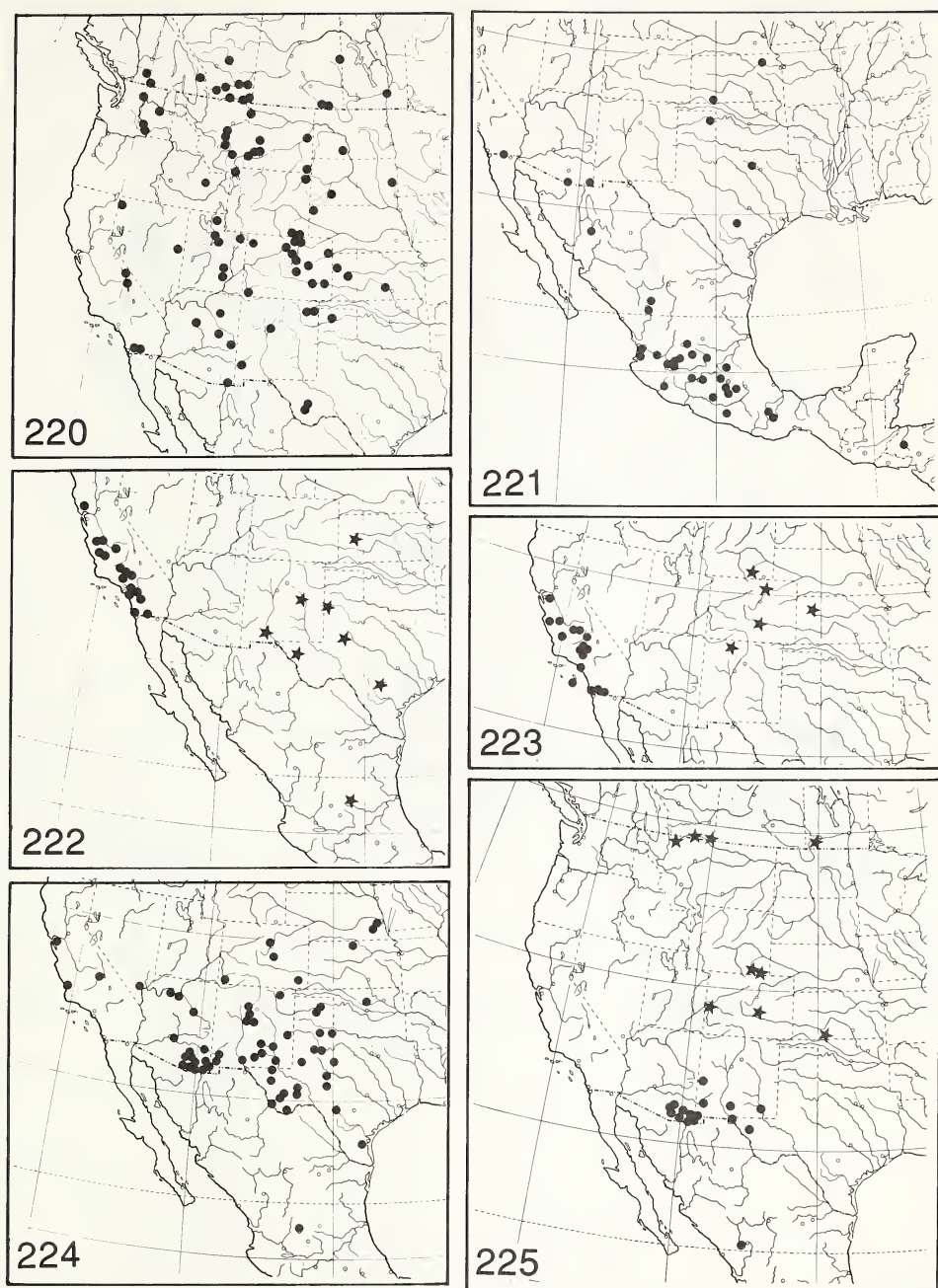
Figures 206–209. Maps illustrating position of collecting localities for: 206, *Apleurus saginatus*; 207, *A. lutulentus*; 208, *A. jacobinus*; 209, *A. albovestitus*.
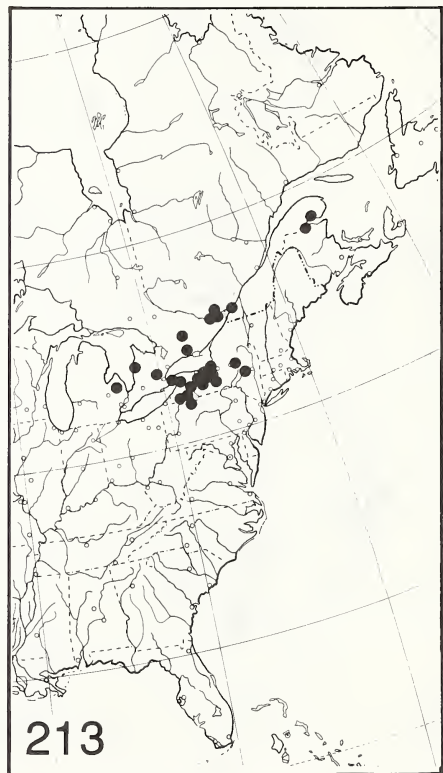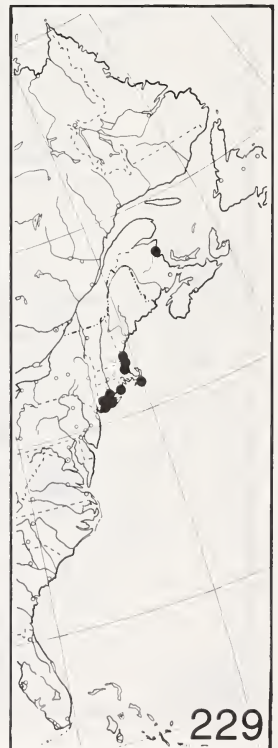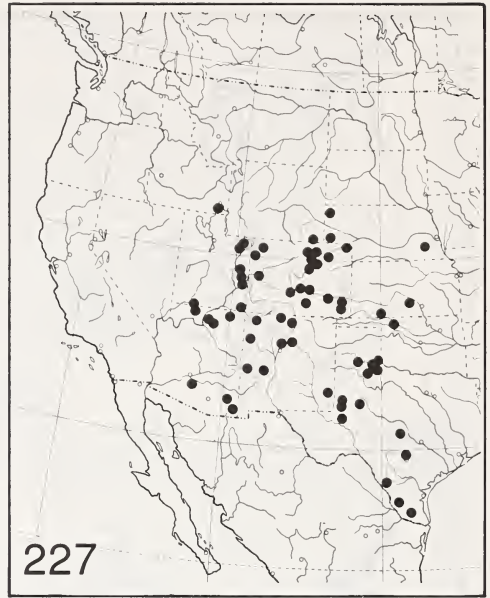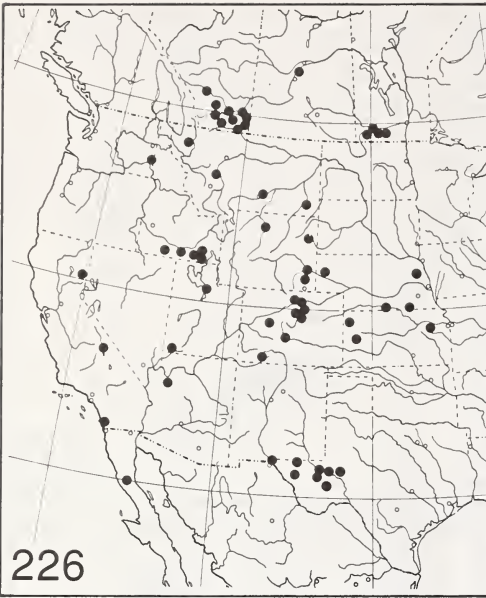
Figures 210–213, Maps illustrating position of collecting localities for: 210, *Apleurus aztecus* (dots) and *A. porosus* (stars); 211, *A. angularis*; 212, *A. hystrix*; 213, *Cleonis pigra*.

Figures 214–219. Maps illustrating position of collecting localities for: 214, *Cleonidius longinasus*; 215, *C. subcylindricus*; 216, *C. eustictorrhinus*; 217, *C. pleuralis*; 218, *C. texanus*; 219, *C. erysimi*.

Figures 220–225. Maps illustrating position of collecting localities for: 220, *Cleonidius trivittatus*; 221, *C. boucardi*; 222, *C. placidus* (dots) and *C. infrequens* (stars); 223, *C. americanus* (dots) and *C. collaris* (stars); 224, *C. quadrilineatus*; 225, *C. notolomus* (dots) and *C. puberulus* (stars).

Figures 226–229. Maps illustrating position of collecting localities for: 226, *Cleonidius frontalis*; 227, *C. canescens*; 228, *C. poricollis*; 229, *C. calandroides*.
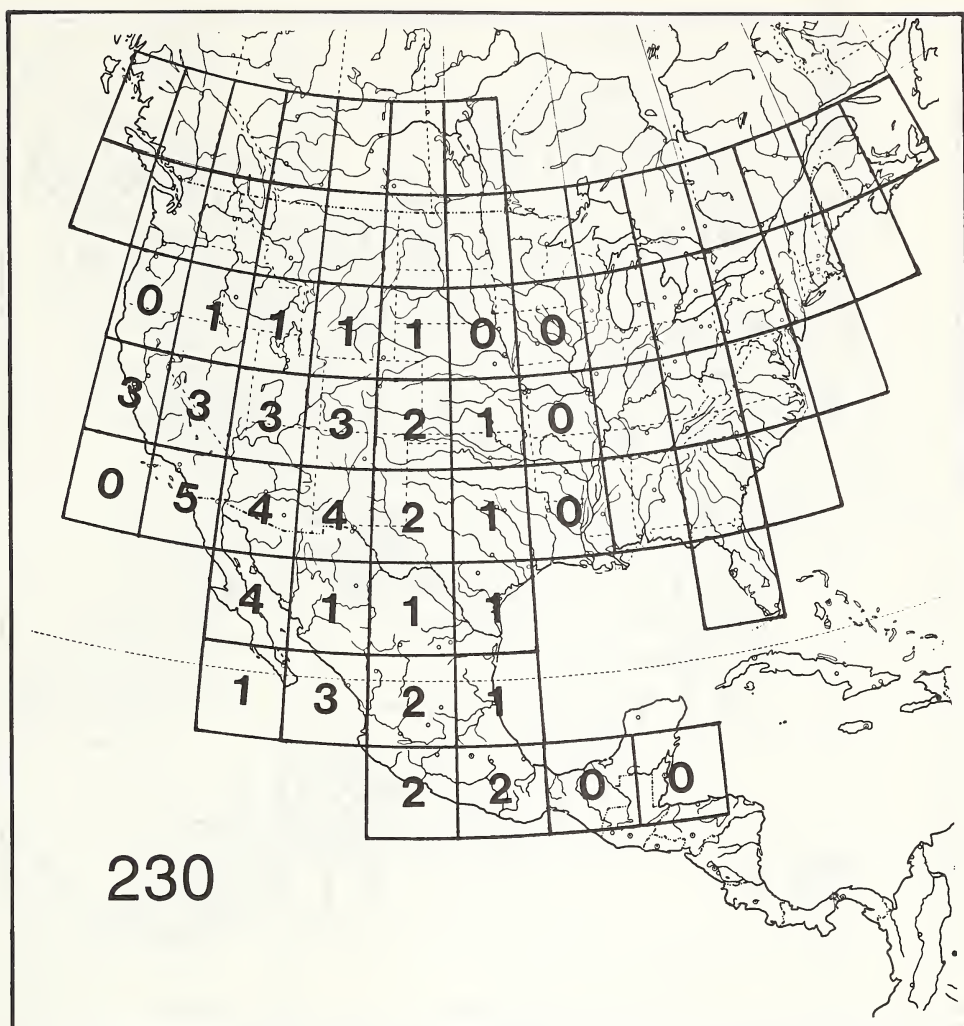
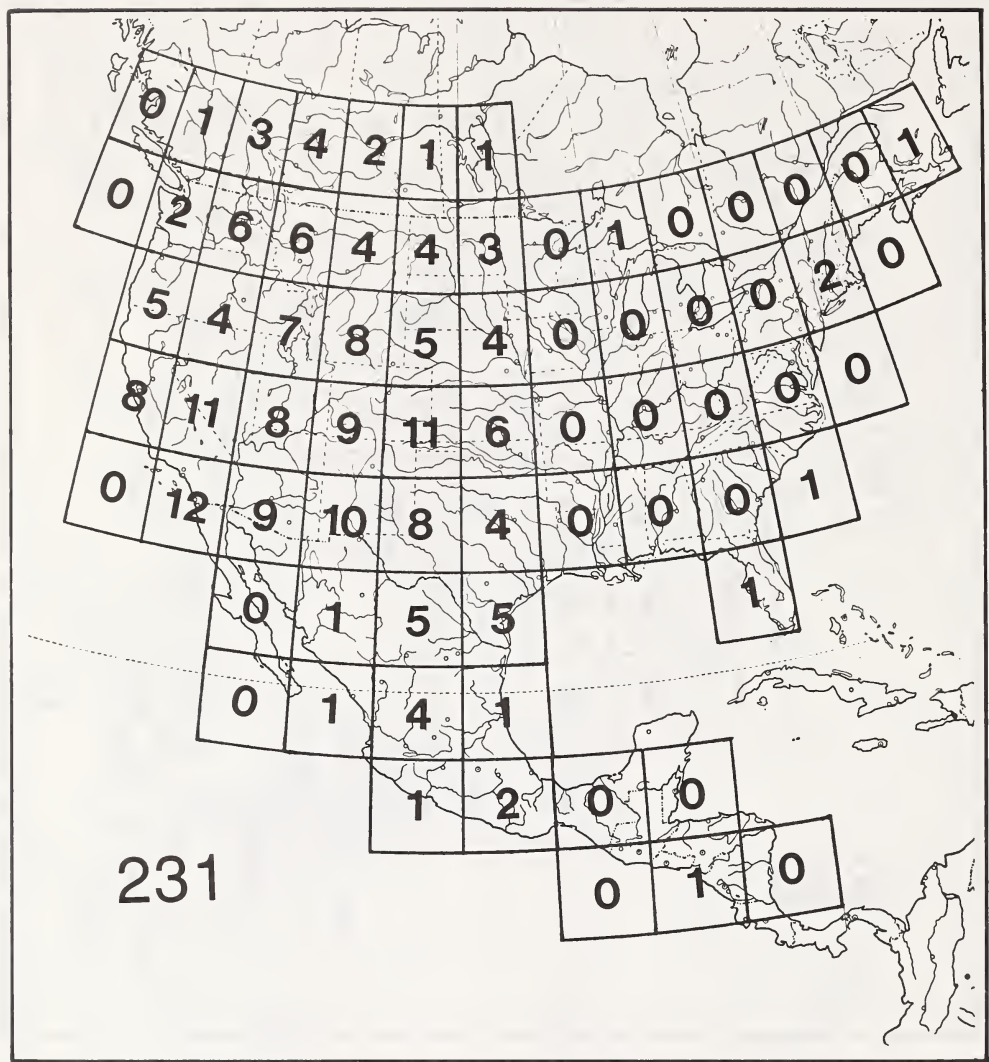Figure 230. Numbers of species of *Apleurus* in 5° intervals.

Figure 231. Numbers of species of *Cleonidius* in 5° intervals.
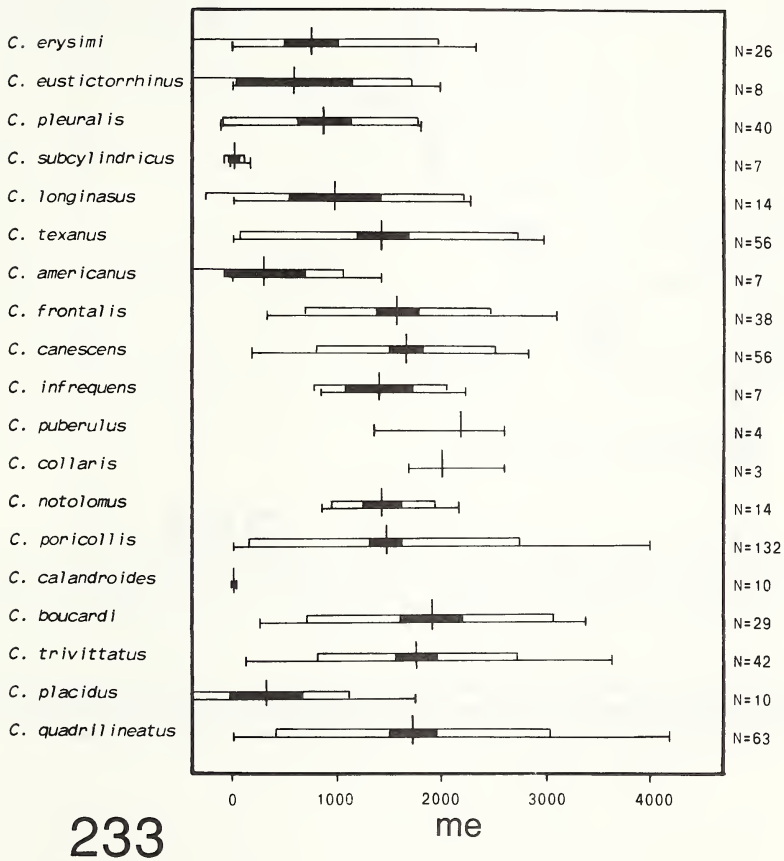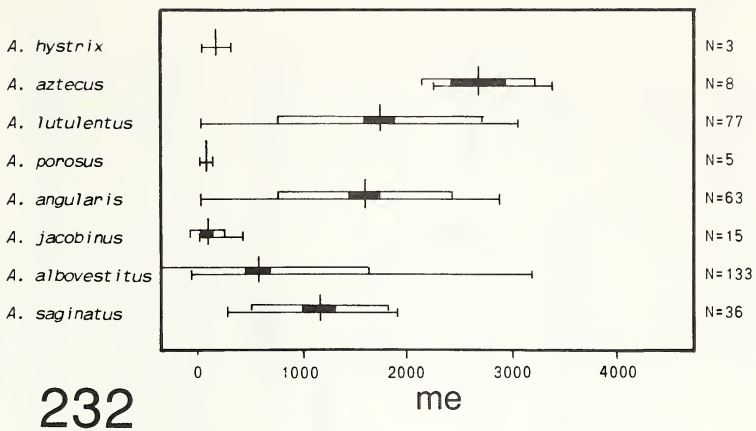
Figures 232–233. Hubbs-Hubbs diagrams illustrating variation among specimens of: 232, *Apleurus* species; elevation; 233, *Cleonidius* species; elevation. See caption for Fig. 49 for explanation.
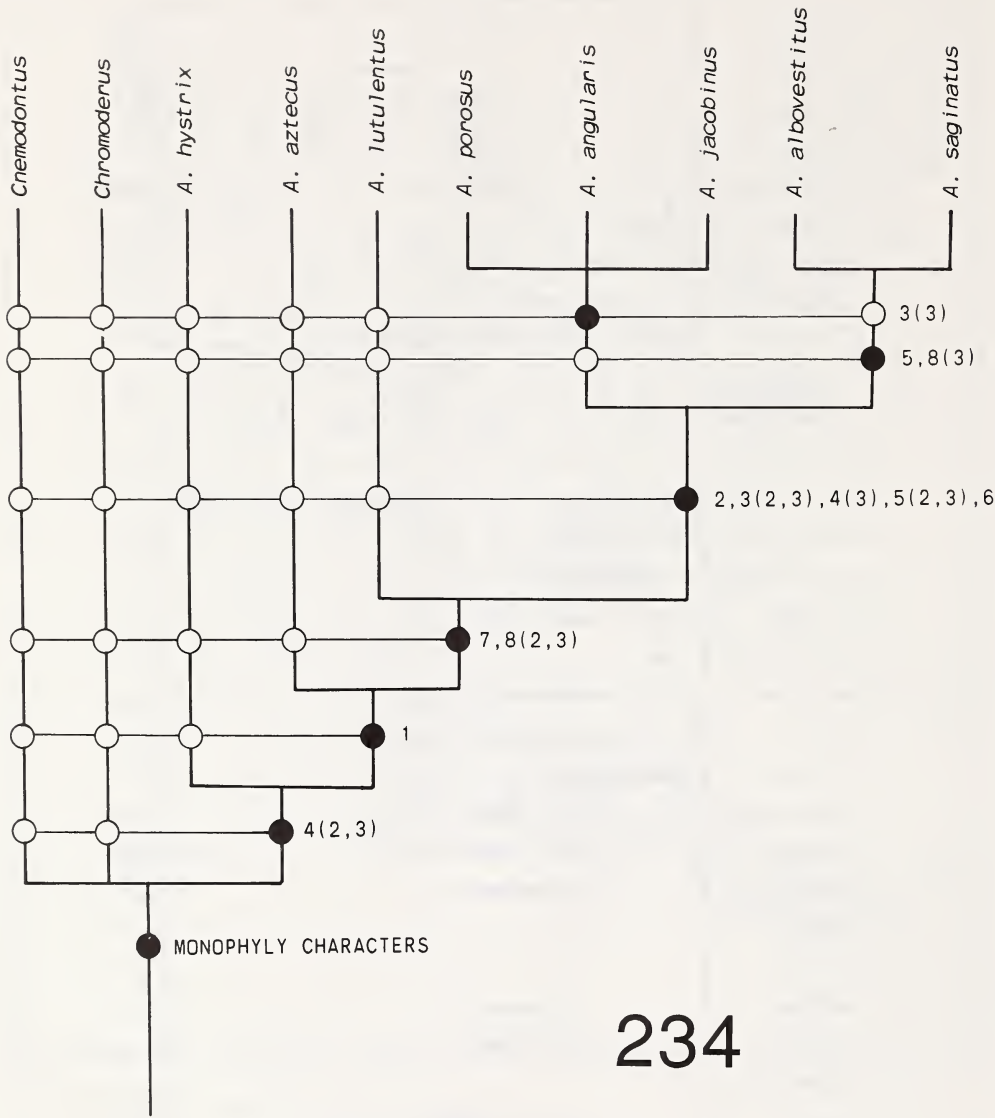
Figure 234. Reconstructed phylogeny based on primary characters illustrating hypothesized phylogenetic relationships among *Apleurus* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables I and II for discussion of characters and states (numbers in parentheses).
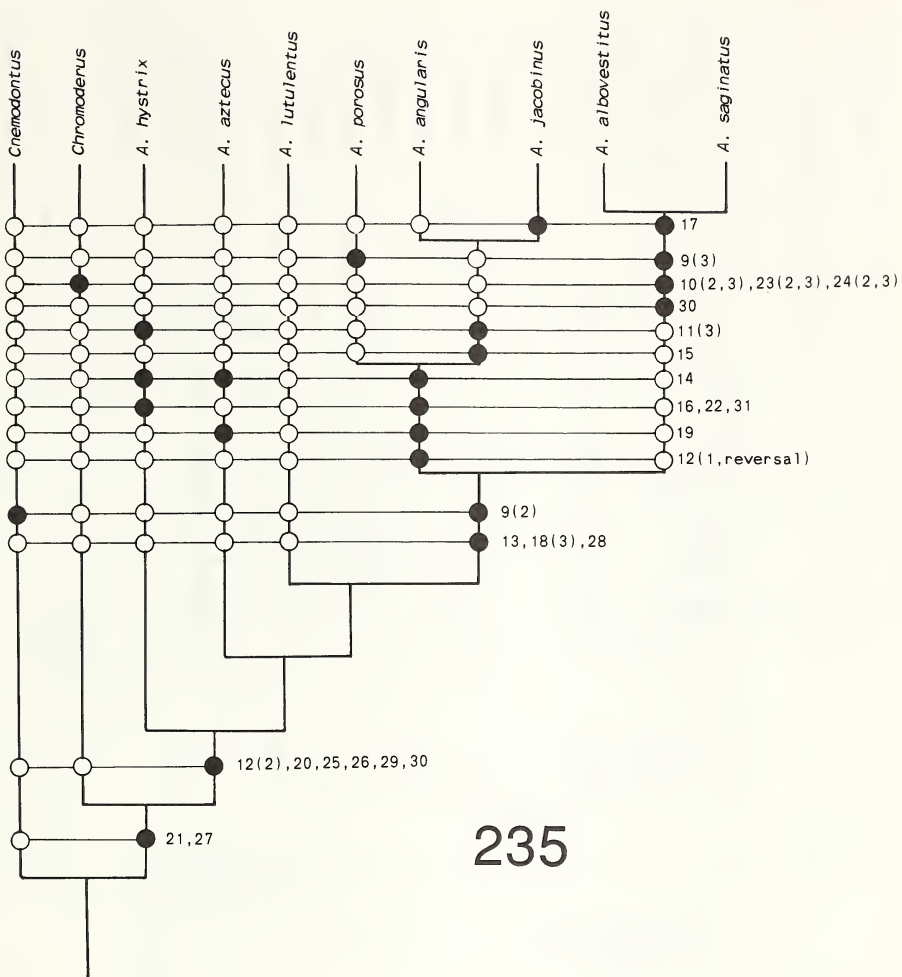
Figure 235. Reconstructed phylogeny based on primary and secondary characters illustrating hypothesized phylogenetic relationships among *Apleurus* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables I and II for discussion of characters and states (numbers in parentheses).
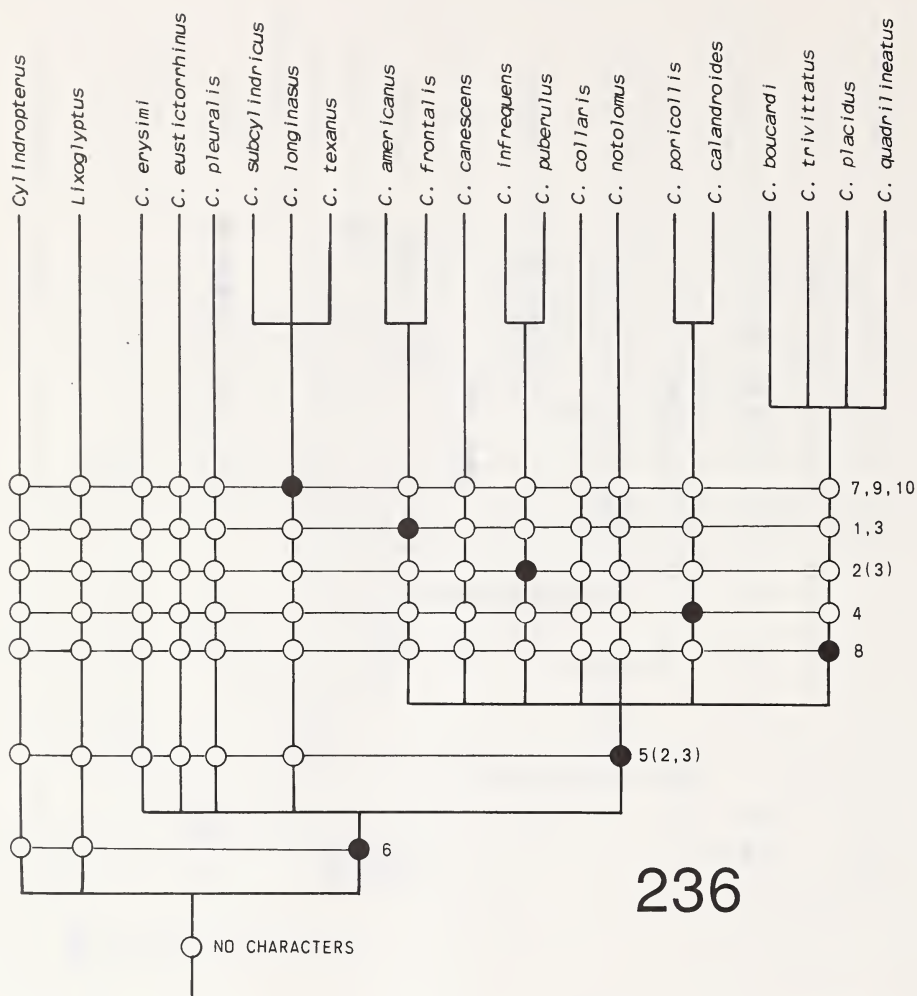
Figure 236. Reconstructed phylogeny based on primary characters illustrating hypothesized phylogenetic relationships among *Cleonidius* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables III and IV for discussion of characters and states (numbers in parentheses).
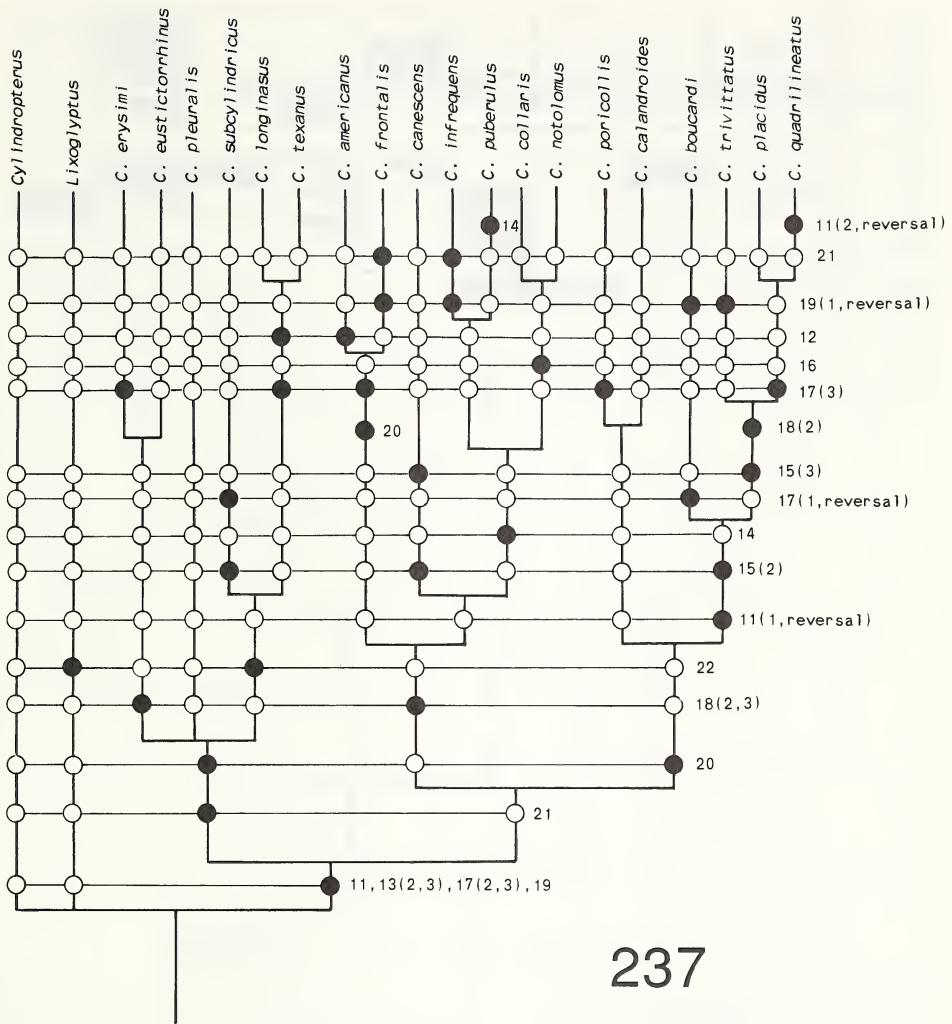
Figure 237. Reconstructed phylogeny based on primary and secondary characters illustrating hypothesized phylogenetic relationships among *Cleonidius* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables III and IV for discussion of characters and states (numbers in parentheses).
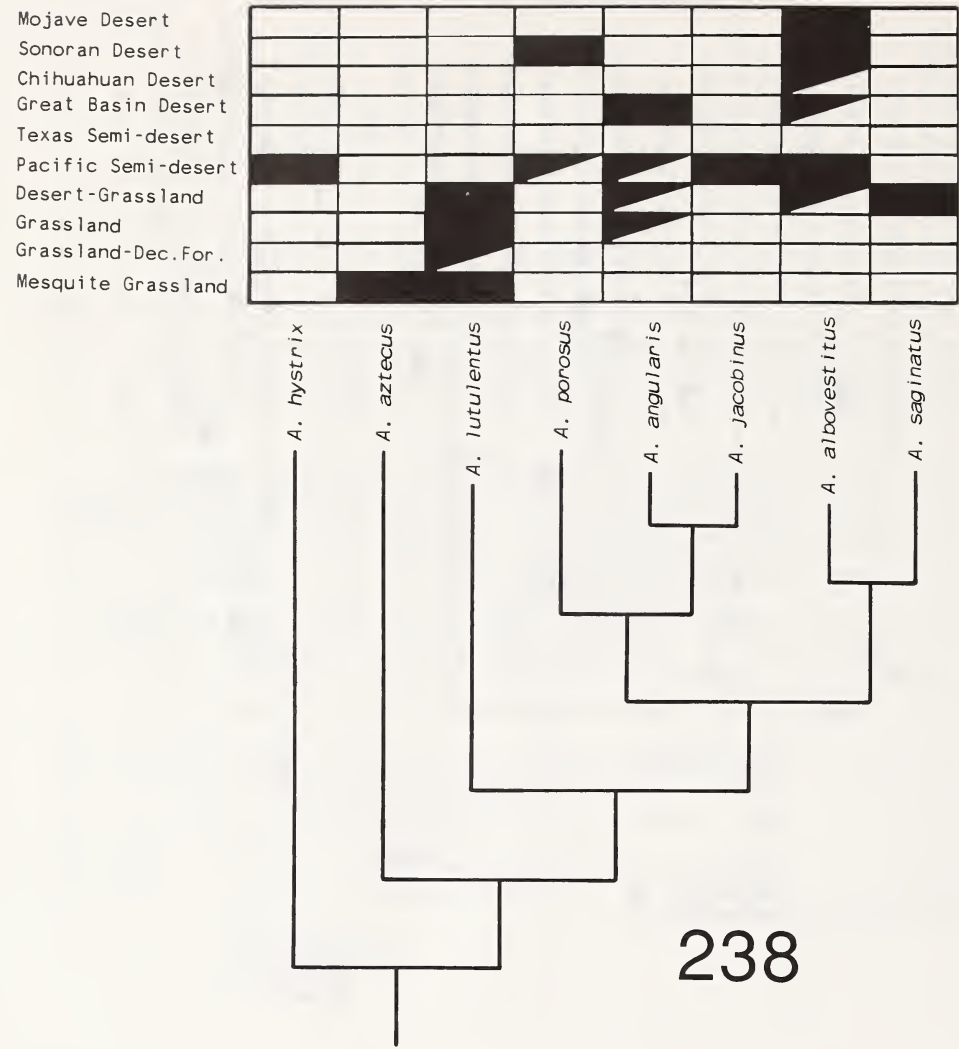
Figure 238. Habitat associations of *Apleurus* species Solid box denotes marked association, half-box slight association. Phylogeny following 235.

Figure 239. Plant associations of *Apleurus* species Solid box denotes marked association, half-box slight association, check mark few collection records. Plant taxa are listed alphabetically. Phylogeny following 235.
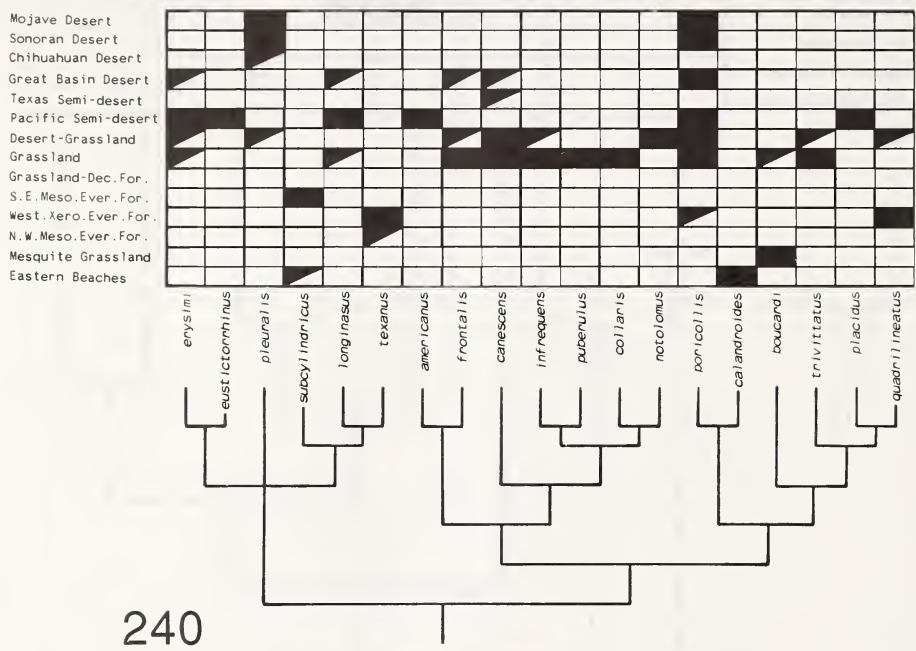
Figure 240. Habitat associations of *Cleonidius* species Solid box denotes marked association, half-box slight association. Phylogeny following 237.
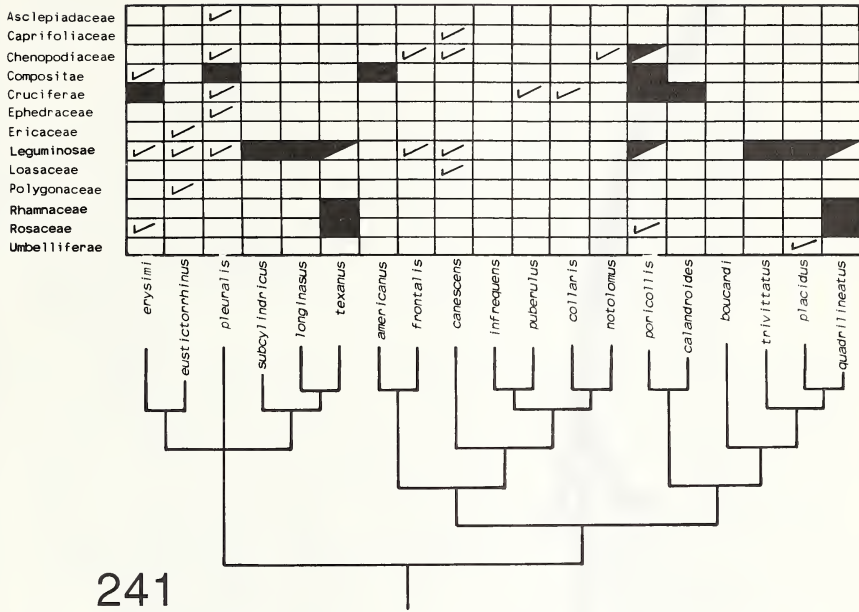
Figure 241. Plant associations of *Cleonidius* species. Solid box denotes marked association, half-box slight association, check mark few collection records. Plant associations are unknown for some species. Plant taxa are listed alphabetically. Phylogeny following 237.
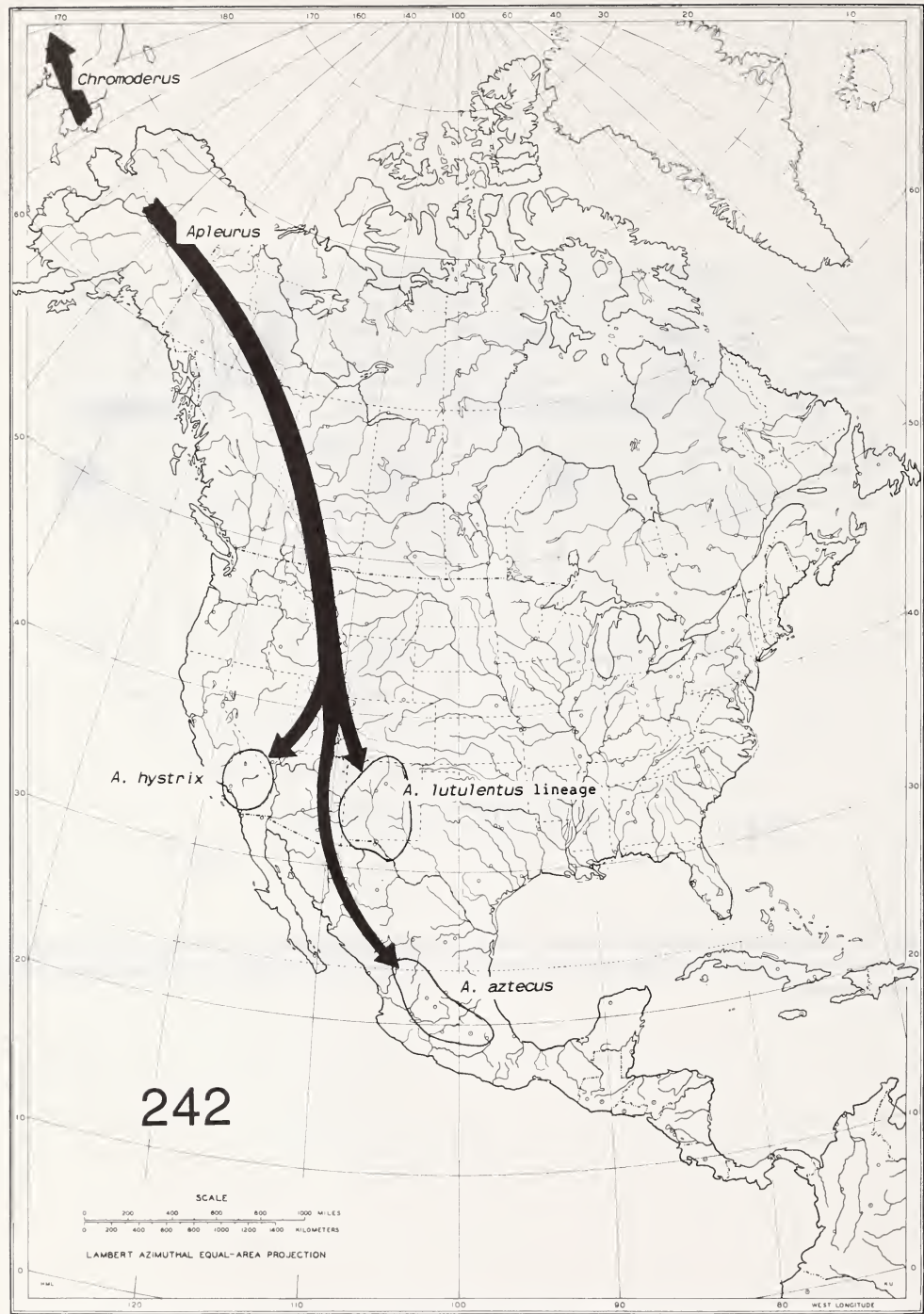
Figure 242. Origin and initial diversification of *Apleurus* in North America: *A. hystrix*, *A. aztecus*, and *A. lutulentus-A. porosus-A. angularis-A. jacobinus-A. albovestitus-A. saginatus* lineage. See text for detailed explanation.
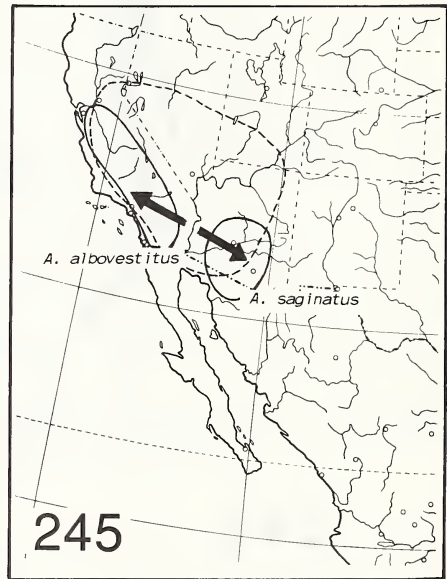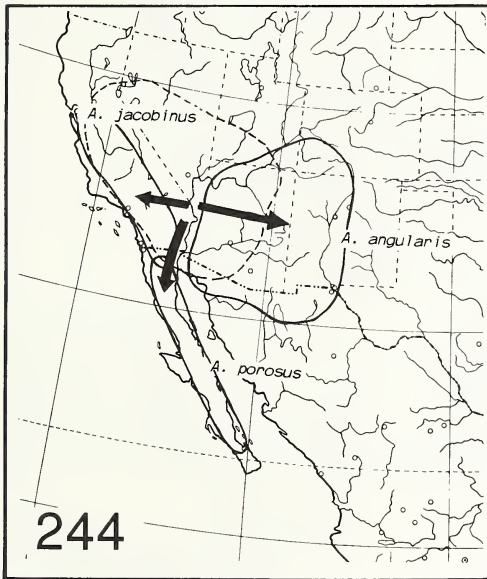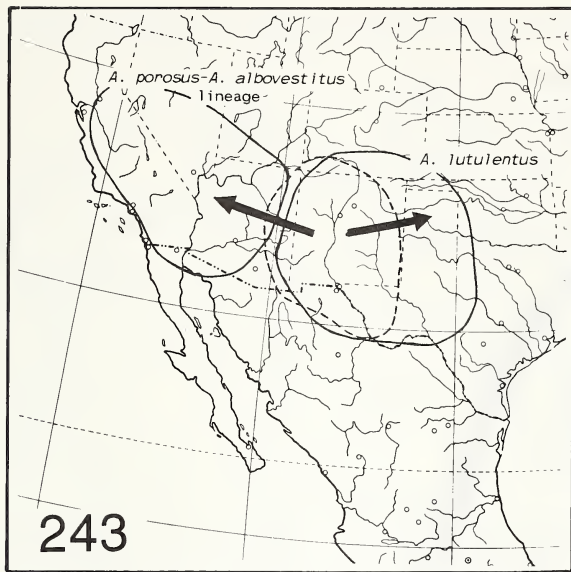
Figures 243–245. Diversification of *Apleurus* in North America (see text for detailed explanation; dashed lines indicate hypothesized ancestral distribution, solid lines indicate present distributions. 243, *A. lutulentus* and *A. porosus-A. angularis-A. jacobinus-A. albovestitus-A. saginatus* lineage; 244, *A. angularis*, *A. jacobinus* and *A. porosus*; 245, *A. albovestitus* and *A. saginatus*.
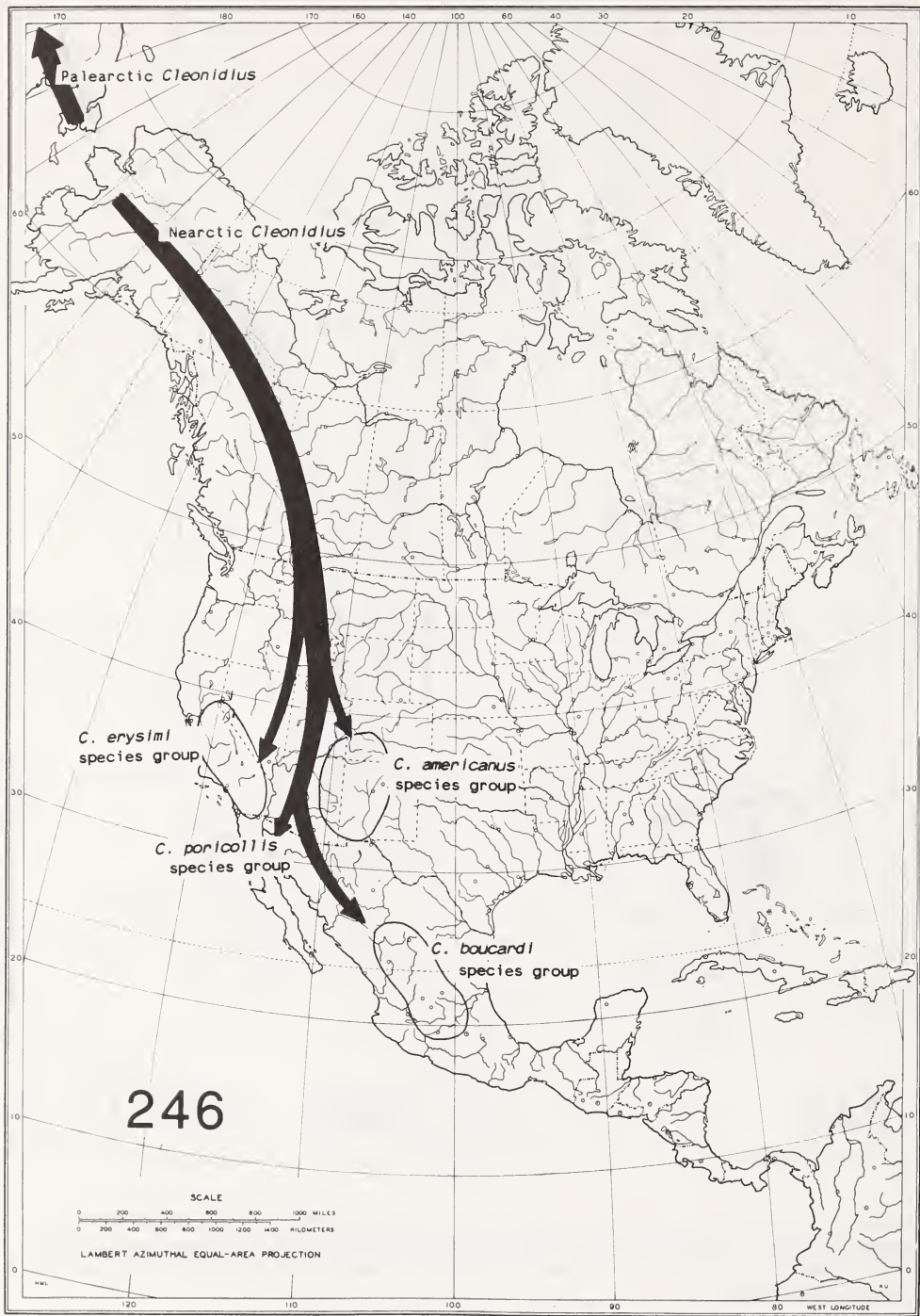
Figure 246. Origin and initial diversification of *Cleonidius* in North America: *Cleonidius erysimi* group, *C. americanus* group, *C. poricollis* group, and *C. boucardi* group. See text, and caption for 242 for detailed explanation.
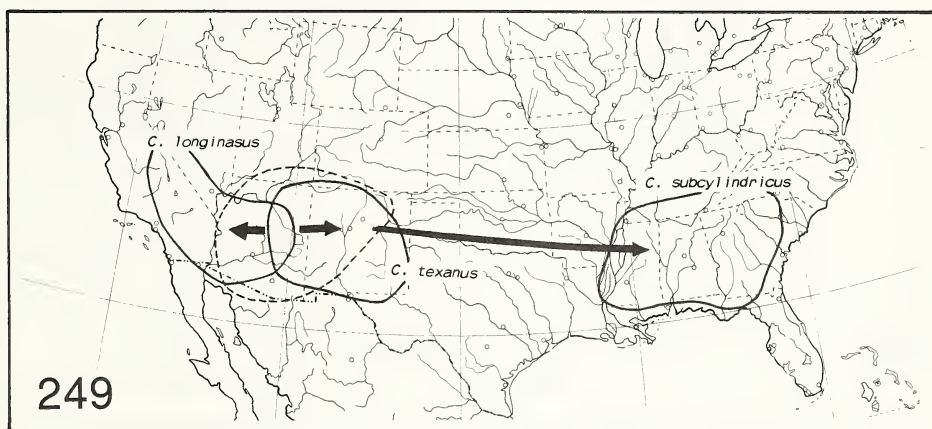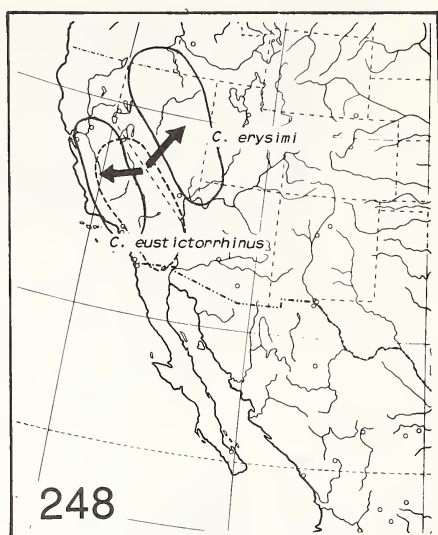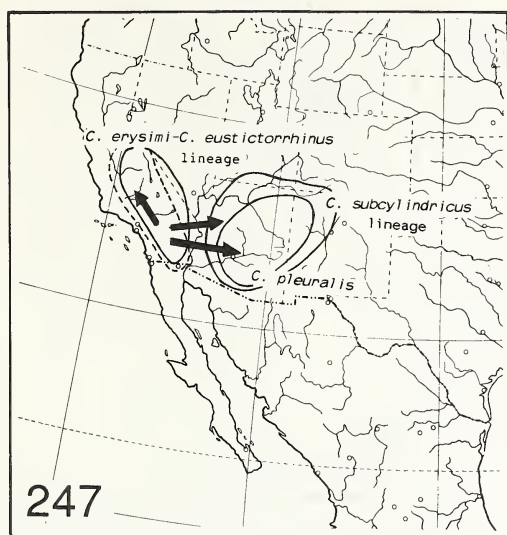
Figures 247–249. Diversification of *Cleonidius* in North America. See text, and captions for 243–245 for detailed explanation. 247, *C. erysimi-C. eustictorrhinus*, *C. pleuralis*, and *C. subcylindricus-C. longinasus-C. texanus* lineages; 248, *C. erysimi* and *C. eustictorrhinus*; 249, *C. subcylindricus*, *C. longinasus* and *C. texanus*.
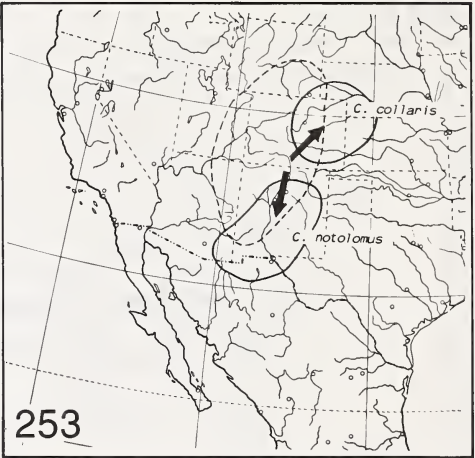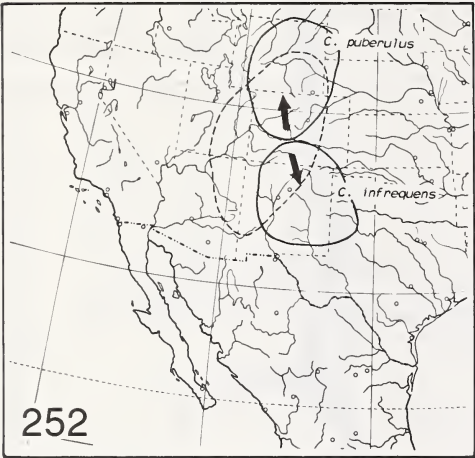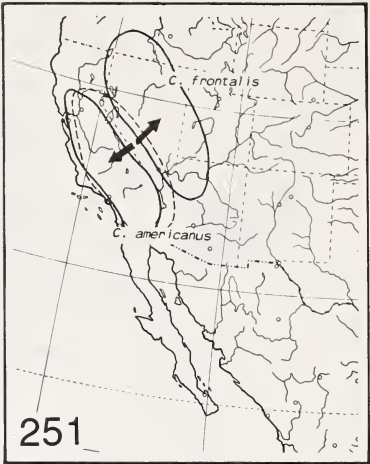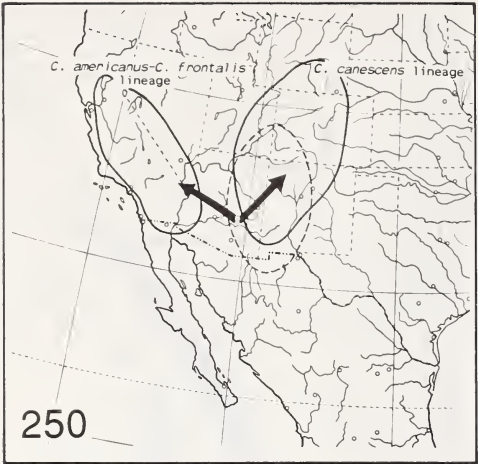
Figures 250–253. Diversification of *Cleonidius* in North America. See text, and captions for 243–245 for detailed explanation. 250, *Cleonidius americanus-C. frontalis, C. canescens-C. infrequens-C. puberulus-C. collaris-C. notolomus* lineages; 251, *C. americanus* and *C. frontalis*; 252, *C. puberulus* and *C. infrequens*; 253, *C. collaris* and *C. notolomus*.
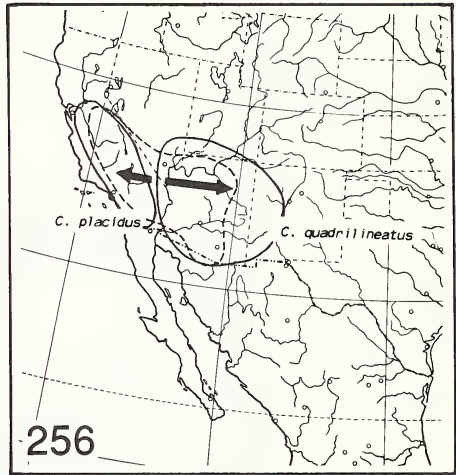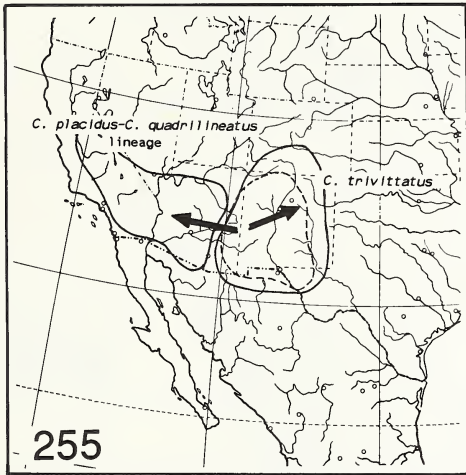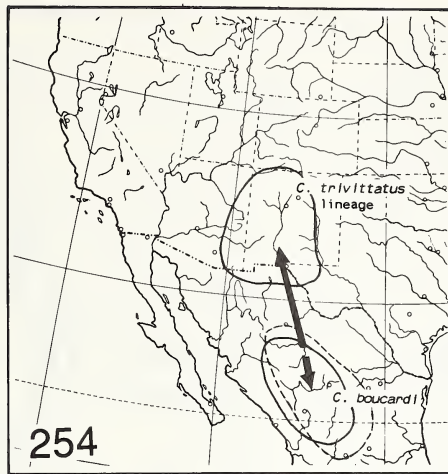
Figures 254–256. Diversification of *Cleonidius* in North America. See text, and captions for 243–245 for detailed explanation. 254, *Cleonidius boucardi* and *C. trivittatus-C. placidus-C. quadrilineatus* lineage; 255, *C. trivittatus* and *C. placidus-C. quadrilineatus* lineage; 256, *C. placidus* and *C. quadrilineatus*.
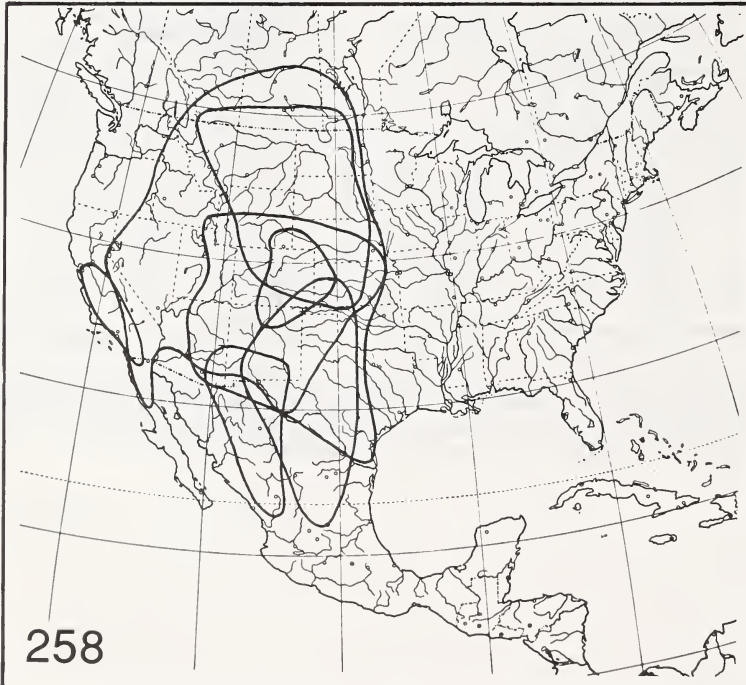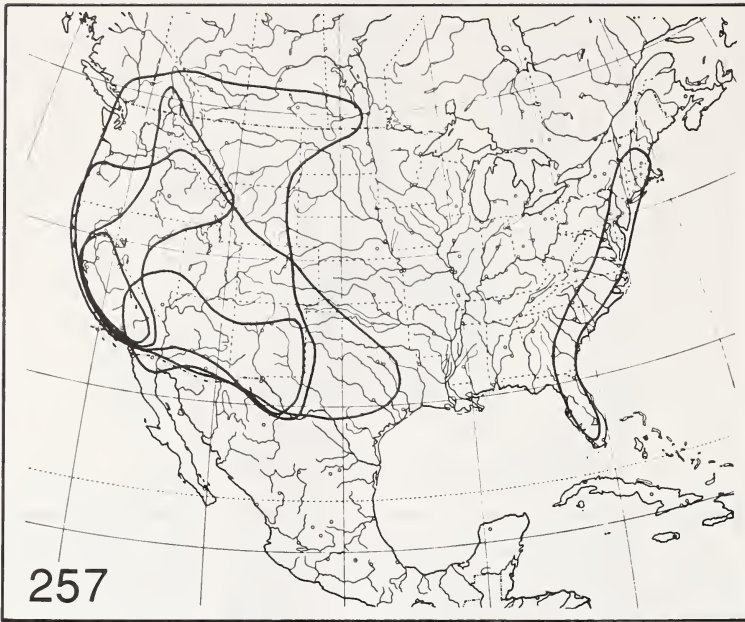
Figures 257–258. Geographic ranges of species in: 257, *Cleonidius erysimi* species group; 258, *C. americanus* species group.
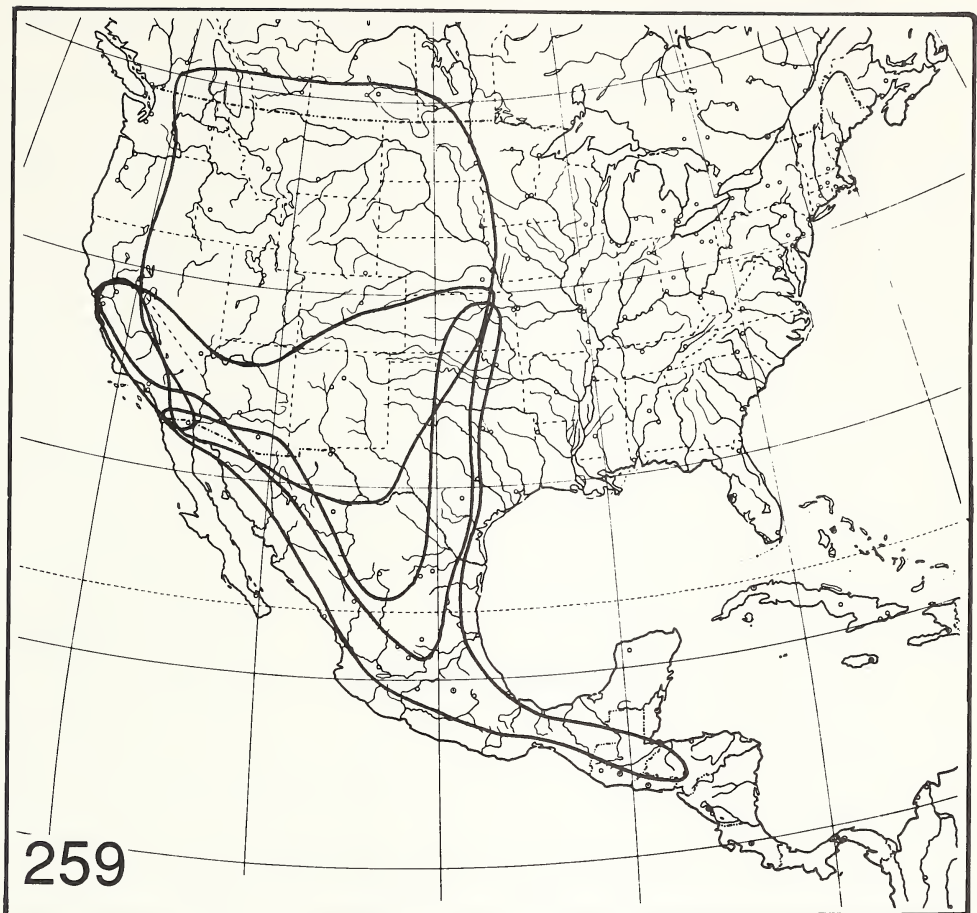
259. Geographic ranges of species in the *Cleonidius boucardi* species group

APPENDIX 1: Tables 1–33

Table 1. Descriptive statistics for *S. confusus* based on eight males and eight females from Medicine Hat, Alberta

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.60 – 2.20	1.900	0.278	0.131
WF	1.60 – 2.20	1.938	0.299	0.141
WRA	1.50 – 2.00	1.713	0.246	0.116
LP	2.40 – 3.40	2.913	0.477	0.225
WPB	3.00 – 4.30	3.725	0.698	0.329
WElH	3.80 – 5.30	4.638	0.810	0.382
WElM	4.60 – 6.40	5.550	0.935	0.441
LEl	6.90 – 9.90	8.350	1.425	0.672
LEy	1.30 – 1.70	1.513	0.246	0.116
WEy	0.60 – 0.80	0.763	0.112	0.053
B. Proportions.				
WEy/LEy	0.46 – 0.57	0.506	0.058	0.027
WPB/LP	1.23 – 1.40	1.278	0.080	0.038
WRA/LR	0.85 – 0.95	0.902	0.060	0.028
WRA/WF	0.81 – 0.94	0.886	0.059	0.027
WElM/LEl	0.64 – 0.72	0.665	0.036	0.017
LP/LEl	0.33 – 0.36	0.349	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.80 – 2.30	2.113	0.233	0.110
WF	1.80 – 2.40	2.150	0.289	0.136
WRA	1.50 – 2.00	1.838	0.265	0.125
LP	2.70 – 3.50	3.213	0.396	0.186
WPB	3.30 – 4.60	4.113	0.682	0.321
WElH	4.20 – 5.80	5.175	0.768	0.362
WElM	5.00 – 7.00	6.163	0.948	0.447
LEl	7.80 –10.10	9.325	1.048	0.493
LEy	1.40 – 1.80	1.613	0.187	0.088
WEy	0.70 – 0.90	0.800	0.113	0.053
B. Proportions				
WEy/LEy	0.47 – 0.53	0.496	0.029	0.013
WPB/LP	1.22 – 1.35	1.278	0.070	0.033
WRA/LR	0.81 – 0.91	0.869	0.064	0.030
WRA/WF	0.81 – 0.90	0.855	0.042	0.020
WElM/LEl	0.62 – 0.71	0.660	0.042	0.019
LP/LEl	0.33 – 0.36	0.344	0.013	0.006

Table 2. Descriptive statistics for *S. cristaticollis* based on one male and one female from Medicine Hat, Alberta

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	2.10	2.10	–	–
WF	2.10	2.10	–	–
WRA	1.80	1.80	–	–
LP	3.30	3.30	–	–
WPB	4.10	4.10	–	–
WElH	5.40	5.40	–	–
WElM	6.40	6.40	–	–
LEl	10.20	10.20	–	–
LEy	1.70	1.70	–	–
WEy	0.80	0.80	–	–
B. Proportions.				
WEy/LEy	0.47	0.47	–	–
WPB/LP	1.24	1.24	–	–
WRA/LR	0.86	0.86	–	–
WRA/WF	0.86	0.86	–	–
WElM/LEl	0.64	0.64	–	–
LP/LEl	0.32	0.32	–	–
Female				
A. Measurements, in mm.				
LR	2.10	2.10	–	–
WF	2.20	2.20	–	–
WRA	1.90	1.90	–	–
LP	3.40	3.40	–	–
WPB	4.30	4.30	–	–
WElH	5.60	5.60	–	–
WElM	6.60	6.60	–	–
LEl	10.20	10.2	–	–
LEy	1.80	1.80	–	–
WEy	0.80	0.80	–	–
B. Proportions.				
WEy/LEy	0.44	0.44	–	–
WPB/LP	1.27	1.27	–	–
WRA/LR	0.91	0.91	–	–
WRA/WF	0.86	0.86	–	–
WElM/LEl	0.65	0.65	–	–
LP/LEl	0.33	0.33	–	–

Table 3. Descriptive statistics for *S. immaculatus* based on eight males and eight females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.00 – 2.30	2.138	0.195	0.092
WF	1.80 – 2.00	1.950	0.113	0.053
WRA	1.60 – 2.00	1.850	0.196	0.092
LP	2.90 – 3.40	3.163	0.310	0.146
WPB	3.80 – 4.40	4.138	0.288	0.136
WElH	4.80 – 5.80	5.400	0.488	0.230
WElM	5.50 – 6.60	6.238	0.555	0.262
LEl	9.00 –10.90	10.112	0.850	0.400
LEy	1.40 – 1.80	1.588	0.169	0.080
WEy	0.70 – 0.90	0.800	0.080	0.038
B. Proportions.				
WEy/LEy	0.50 – 0.53	0.504	0.018	0.008
WPB/LP	1.24 – 1.40	1.310	0.078	0.037
WRA/LR	0.80 – 0.95	0.866	0.069	0.033
WRA/WF	0.89 – 1.00	0.948	0.072	0.034
WElM/LEl	0.58 – 0.64	0.617	0.030	0.014
LP/LEl	0.30 – 0.34	0.313	0.019	0.009
Females				
A. Measurements, in mm.				
LR	2.20 – 2.40	2.275	0.133	0.063
WF	2.00 – 2.40	2.150	0.196	0.092
WRA	1.90 – 2.10	2.000	0.139	0.065
LP	3.20 – 3.60	3.438	0.226	0.106
WPB	4.20 – 4.70	4.425	0.328	0.155
WElH	5.50 – 6.40	6.000	0.488	0.230
WElM	6.30 – 7.30	6.788	0.522	0.246
LEl	9.40 –12.00	11.075	1.254	0.591
LEy	1.50 – 1.80	1.675	0.155	0.073
WEy	0.80 – 1.00	0.900	0.113	0.053
B. Proportions.				
WEy/LEy	0.47 – 0.60	0.538	0.069	0.032
WPB/LP	1.19 – 1.44	1.289	0.121	0.057
WRA/LR	0.79 – 0.96	0.880	0.072	0.034
WRA/WF	0.88 – 1.05	0.932	0.081	0.038
WElM/LEl	0.56 – 0.67	0.614	0.047	0.022
LP/LEl	0.30 – 0.35	0.311	0.027	0.012

Table 4. Descriptive statistics for *S. parshus* based on eight males and eight females from southern Manitoba and Ontario

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	1.70 – 2.10	1.850	0.196	0.013
WF	1.50 – 1.90	1.675	0.192	0.091
WRA	1.30 – 1.60	1.488	0.187	0.088
LP	2.50 – 3.00	2.725	0.275	0.130
WPB	3.00 – 3.80	3.363	0.453	0.214
WElH	3.80 – 5.30	4.450	0.717	0.338
WElM	4.50 – 5.80	5.025	0.825	0.388
LEl	7.20 – 8.60	7.913	0.909	0.428
LEy	1.20 – 1.50	1.350	0.179	0.084
WEy	0.60 – 0.80	0.688	0.125	0.059
B. Proportions.				
WEy/LEy	0.46 – 0.58	0.509	0.060	0.028
WPB/LP	1.15 – 1.31	1.233	0.079	0.037
WRA/LR	0.76 – 0.84	0.804	0.055	0.026
WRA/WF	0.81 – 0.94	0.889	0.071	0.034
WElM/LEl	0.61 – 0.68	0.634	0.042	0.020
LP/LEl	0.33 – 0.37	0.345	0.016	0.007
Females				
A. Measurements, in mm.				
LR	1.70 – 2.20	1.913	0.233	0.110
WF	1.60 – 1.90	1.738	0.178	0.084
WRA	1.40 – 1.70	1.550	0.160	0.076
LP	2.60 – 3.30	2.875	0.399	0.188
WPB	3.20 – 4.00	3.625	0.466	0.220
WElH	4.20 – 5.40	4.838	0.708	0.334
WElM	4.70 – 6.20	5.400	0.765	0.360
LEl	7.50 – 9.60	8.613	1.132	0.534
LEy	1.30 – 1.60	1.425	0.175	0.082
WEy	0.60 – 0.80	0.738	0.112	0.053
B. Proportions.				
WEy/LEy	0.46 – 0.54	0.517	0.041	0.019
WPB/LP	1.18 – 1.36	1.262	0.076	0.036
WRA/LR	0.77 – 0.84	0.812	0.041	0.020
WRA/WF	0.88 – 0.94	0.892	0.030	0.014
WElM/LEl	0.59 – 0.65	0.627	0.028	0.013
LP/LEl	0.32 – 0.35	0.334	0.018	0.008

Table 5. Descriptive statistics for *S. plumbeus* based on eight males and eight females from Rivière – au – Tonnerre, Québec

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	1.70 – 1.90	1.844	0.109	0.048
WF	1.60 – 1.80	1.722	0.125	0.055
WRA	1.40 – 1.70	1.567	0.130	0.058
LP	2.50 – 3.00	2.700	0.281	0.125
WPB	3.00 – 3.60	3.356	0.368	0.164
WElH	4.10 – 5.20	4.600	0.618	0.275
WElM	4.60 – 5.60	5.067	0.586	0.260
LEl	7.40 – 9.00	8.233	0.891	0.396
LEy	1.20 – 1.50	1.356	0.170	0.075
WEy	0.70 – 0.90	0.767	0.106	0.047
B. Proportions.				
WEy/LEy	0.50 – 0.64	0.567	0.068	0.030
WPB/LP	1.20 – 1.32	1.243	0.062	0.028
WRA/LR	0.82 – 0.90	0.849	0.038	0.017
WRA/WF	0.88 – 0.94	0.910	0.045	0.020
WElM/LEl	0.60 – 0.64	0.615	0.015	0.007
LP/LEl	0.31 – 0.34	0.328	0.012	0.005
Females				
A. Measurements, in mm.				
LR	1.80 – 2.40	2.100	0.287	0.145
WF	1.90 – 2.00	1.971	0.073	0.037
WRA	1.70 – 2.00	1.786	0.160	0.081
LP	2.80 – 3.30	3.057	0.272	0.137
WPB	3.60 – 4.20	3.886	0.351	0.177
WElH	4.90 – 6.00	5.386	0.551	0.277
WElM	5.40 – 6.60	5.857	0.567	0.286
LEl	9.10 –11.00	9.957	1.017	0.512
LEy	1.30 – 1.60	1.486	0.182	0.092
WEy	0.70 – 0.80	0.757	0.080	0.040
B. Proportions.				
WEy/LEy	0.44 – 0.57	0.511	0.063	0.032
WPB/LP	1.22 – 1.32	1.272	0.054	0.027
WRA/LR	0.82 – 0.94	0.853	0.065	0.033
WRA/WF	0.85 – 1.00	0.906	0.068	0.034
WElM/LEl	0.57 – 0.62	0.589	0.030	0.015
LP/LEl	0.29 – 0.33	0.307	0.021	0.010

Table 6. Descriptive statistics for *S. stenothorax* based on eight males and eight females from Bluefish Caves Archaeological Site, Yukon Territory

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	1.80 – 2.10	1.975	0.133	0.063
WF	1.80 – 2.10	2.000	0.139	0.065
WRA	1.70 – 1.90	1.813	0.096	0.045
LP	2.60 – 2.90	2.825	0.155	0.073
WPB	3.50 – 3.90	3.700	0.196	0.093
WElH	4.60 – 5.40	5.025	0.365	0.172
WElM	5.30 – 6.10	5.688	0.388	0.183
LEl	9.00 –10.40	9.713	0.745	0.351
LEy	1.60 – 1.80	1.713	0.125	0.059
WEy	0.80 – 0.90	0.875	0.069	0.033
B. Proportions.				
WEy/LEy	0.47 – 0.56	0.512	0.042	0.020
WPB/LP	1.24 – 1.35	1.310	0.051	0.024
WRA/LR	0.90 – 0.95	0.918	0.036	0.017
WRA/WF	0.86 – 0.95	0.907	0.044	0.020
WElM/LEl	0.57 – 0.60	0.586	0.017	0.008
LP/LEl	0.28 – 0.32	0.291	0.020	0.009
Females				
A. Measurements, in mm.				
LR	1.80 – 2.10	1.988	0.169	0.080
WF	1.90 – 2.20	2.088	0.169	0.080
WRA	1.70 – 2.00	1.888	0.169	0.080
LP	2.70 – 3.20	2.988	0.233	0.110
WPB	3.50 – 4.20	3.925	0.356	0.168
WElH	4.70 – 5.80	5.388	0.575	0.271
WElM	5.40 – 6.40	6.088	0.450	0.212
LEl	9.60 –11.50	10.512	0.930	0.438
LEy	1.50 – 1.90	1.750	0.212	0.100
WEy	0.80 – 0.90	0.863	0.078	0.037
B. Proportions.				
WEy/LEy	0.47 – 0.53	0.494	0.031	0.015
WPB/LP	1.27 – 1.36	1.314	0.042	0.020
WRA/LR	0.90 – 1.00	0.950	0.040	0.019
WRA/WF	0.86 – 0.95	0.904	0.038	0.018
WElM/LEl	0.55 – 0.61	0.580	0.030	0.014
LP/LEl	0.27 – 0.30	0.284	0.012	0.006

Table 7. Descriptive statistics for *A. hystrix* based on eight males and eight females from the El Segundo Sand Dunes, Los Angeles County, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.08 – 1.56	1.345	0.283	0.133
WF	0.88 – 1.24	1.105	0.181	0.085
WRA	0.88 – 1.12	1.040	0.132	0.062
LP	2.08 – 2.72	2.530	0.384	0.181
WPB	2.00 – 2.80	2.530	0.444	0.209
WPT	2.08 – 2.88	2.560	0.411	0.194
WEIM	2.40 – 3.68	3.280	0.615	0.290
LEl	4.56 – 6.24	5.540	0.918	0.433
B. Proportions.				
WPB/LP	0.96 – 1.06	0.999	0.050	0.024
WPT/WPB	1.00 – 1.04	1.013	0.028	0.013
WRA/LR	0.69 – 0.85	0.780	0.088	0.041
WRA/WF	0.87 – 1.05	0.945	0.090	0.043
WEIM/LEl	0.53 – 0.66	0.592	0.062	0.029
LP/LEl	0.42 – 0.47	0.457	0.024	0.011
Females				
A. Measurements, in mm.				
LR	1.36 – 1.64	1.500	0.124	0.059
WF	1.04 – 1.40	1.230	0.162	0.077
WRA	1.04 – 1.24	1.125	0.113	0.053
LP	2.48 – 3.28	2.800	0.345	0.163
WPB	2.48 – 3.20	2.840	0.333	0.157
WPT	2.56 – 3.28	2.860	0.325	0.153
WEIM	3.12 – 4.24	3.720	0.525	0.247
LEl	5.60 – 7.28	6.280	0.775	0.365
B. Proportions.				
WPB/LP	0.97 – 1.06	1.015	0.060	0.028
WPT/WPB	0.97 – 1.03	1.008	0.038	0.018
WRA/LR	0.70 – 0.82	0.751	0.058	0.028
WRA/WF	0.84 – 1.00	0.918	0.086	0.040
WEIM/LEl	0.54 – 0.64	0.592	0.047	0.022
LP/LEl	0.43 – 0.47	0.446	0.017	0.008

Table 8. Descriptive statistics for *A. aztecus* based on 13 males and six females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	0.96 – 1.52	1.182	0.251	0.093
WF	0.92 – 1.36	1.172	0.224	0.083
WRA	0.80 – 1.20	1.015	0.198	0.073
LP	1.76 – 2.88	2.209	0.607	0.225
WPB	1.84 – 3.20	2.566	0.658	0.244
WPT	1.84 – 3.28	2.622	0.674	0.249
WElM	2.88 – 4.56	3.699	0.856	0.317
LEl	3.60 – 6.40	4.701	1.300	0.481
B. Proportions.				
WPB/LP	1.05 – 1.27	1.165	0.094	0.035
WPT/WPB	1.00 – 1.04	1.021	0.023	0.008
WRA/LR	0.79 – 1.00	0.862	0.081	0.030
WRA/WF	0.82 – 0.92	0.866	0.036	0.013
WElM/LEl	0.70 – 0.90	0.792	0.074	0.028
LP/LEl	0.37 – 0.54	0.473	0.073	0.027
Females				
A. Measurements, in mm.				
LR	0.88 – 1.60	1.387	0.384	0.209
WF	0.96 – 1.52	1.333	0.310	0.169
WRA	0.80 – 1.28	1.147	0.270	0.147
LP	1.52 – 2.88	2.520	0.754	0.411
WPB	1.76 – 3.44	2.947	0.899	0.490
WPT	1.84 – 3.60	3.053	0.928	0.505
WElM	2.56 – 4.80	4.173	1.211	0.659
LEl	3.20 – 6.24	5.413	1.678	0.914
B. Proportions.				
WPB/LP	1.12 – 1.21	1.169	0.053	0.029
WPT/WPB	0.98 – 1.05	1.037	0.046	0.025
WRA/LR	0.78 – 0.91	0.833	0.082	0.045
WRA/WF	0.83 – 0.88	0.859	0.034	0.019
WElM/LEl	0.72 – 0.80	0.774	0.049	0.026
LP/LEl	0.45 – 0.49	0.467	0.022	0.012

Table 9. Descriptive statistics for *A. lutulentus* based on eight males and eight females from 2 mi. NE. Portal, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.44 – 1.76	1.660	0.167	0.079
WF	1.20 – 1.44	1.300	0.140	0.066
WRA	1.04 – 1.28	1.180	0.140	0.066
LP	2.56 – 3.36	3.050	0.478	0.202
WPB	2.72 – 3.52	3.160	0.406	0.191
WPT	2.56 – 3.20	2.930	0.327	0.154
WElM	3.36 – 4.80	4.340	0.693	0.327
LEl	5.92 – 7.04	6.560	0.588	0.277
B. Proportions.				
WPB/LP	1.00 – 1.08	1.037	0.038	0.018
WPT/WPB	0.90 – 0.95	0.928	0.024	0.011
WRA/LR	0.67 – 0.76	0.711	0.045	0.021
WRA/WF	0.87 – 0.94	0.908	0.048	0.023
WElM/LEl	0.57 – 0.72	0.661	0.072	0.034
LP/LEl	0.43 – 0.50	0.464	0.039	0.018
Females				
A. Measurements, in mm.				
LR	1.60 – 1.84	1.750	0.119	0.056
WF	1.20 – 1.44	1.350	0.150	0.070
WRA	1.12 – 1.36	1.250	0.127	0.060
LP	2.80 – 3.44	3.160	0.368	0.174
WPB	2.88 – 3.92	3.350	0.478	0.225
WPT	2.72 – 3.52	3.180	0.419	0.198
WElM	3.92 – 5.20	4.540	0.562	0.265
LEl	6.48 – 7.92	7.110	0.763	0.360
B. Proportions.				
WPB/LP	1.03 – 1.14	1.060	0.056	0.026
WPT/WPB	0.90 – 1.00	0.950	0.052	0.024
WRA/LR	0.67 – 0.74	0.714	0.036	0.017
WRA/WF	0.89 – 0.94	0.926	0.035	0.017
WElM/LEl	0.61 – 0.66	0.639	0.028	0.013
LP/LEl	0.42 – 0.47	0.445	0.028	0.013

Table 10. Descriptive statistics for *A. porosus* based on seven males and eight females from 68.0 km. W. Ejido Viscaino, Baja California Sur, México

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.37 – 3.20	2.904	0.473	0.238
WF	1.86 – 2.32	2.124	0.261	0.132
WRA	1.55 – 2.12	1.887	0.293	0.148
LP	3.82 – 5.57	4.747	0.890	0.448
WPB	4.13 – 5.88	5.189	0.934	0.471
WPT	4.02 – 5.68	4.984	0.864	0.435
WEIM	5.57 – 8.05	7.106	1.266	0.638
LEl	8.46 –11.76	10.467	1.820	0.917
B. Proportions.				
WPB/LP	1.02 – 1.17	1.095	0.088	0.044
WPT/WPB	0.93 – 1.00	0.961	0.041	0.021
WRA/LR	0.61 – 0.68	0.650	0.033	0.017
WRA/WF	0.83 – 0.96	0.887	0.061	0.031
WEIM/LEl	0.65 – 0.70	0.679	0.026	0.013
LP/LEl	0.41 – 0.48	0.454	0.035	0.018
Females				
A. Measurements, in mm.				
LR	2.32 – 3.51	3.095	0.580	0.274
WF	1.86 – 2.63	2.329	0.389	0.183
WRA	1.60 – 2.32	2.006	0.356	0.168
LP	4.02 – 5.68	5.096	0.866	0.408
WPB	4.23 – 6.40	5.549	1.155	0.544
WPT	4.23 – 6.09	5.366	0.960	0.452
WEIM	5.99 – 8.88	7.858	1.508	0.711
LEl	8.46 –13.00	11.430	2.411	1.136
B. Proportions.				
WPB/LP	1.05 – 1.13	1.086	0.054	0.025
WPT/WPB	0.90 – 1.02	0.970	0.058	0.027
WRA/LR	0.62 – 0.69	0.650	0.043	0.020
WRA/WF	0.83 – 0.91	0.861	0.047	0.022
WEIM/LEl	0.65 – 0.73	0.689	0.041	0.019
LP/LEl	0.42 – 0.48	0.448	0.028	0.013

Table 11. Descriptive statistics for *A. angularis* based on 15 males and 10 females from Mercury, Nevada

Character	Range	Mean		1.5SD
Males				
A. Measurements, in mm.				
LR	1.55 – 2.23	1.861	0.283	0.097
WF	1.44 – 1.75	1.615	0.190	0.065
WRA	1.14 – 1.65	1.430	0.239	0.082
LP	2.48 – 3.82	3.111	0.573	0.197
WPB	2.99 – 4.33	3.563	0.606	0.209
WPT	3.20 – 4.54	3.818	0.586	0.201
WElM	3.72 – 5.78	4.918	0.884	0.304
LEl	5.68 – 8.57	7.376	1.183	0.407
B. Proprotions.				
WPB/LP	1.07 – 1.29	1.148	0.081	0.028
WPT/WPB	1.03 – 1.13	1.073	0.045	0.016
WRA/LR	0.66 – 0.84	0.769	0.075	0.026
WRA/WF	0.79 – 0.94	0.884	0.068	0.023
WElM/LEl	0.57 – 0.72	0.670	0.062	0.021
LP/LEl	0.36 – 0.46	0.422	0.034	0.012
Females				
A. Measurements, in mm.				
LR	1.55 – 2.33	1.892	0.356	0.150
WF	1.44 – 1.86	1.651	0.208	0.088
WRA	1.24 – 1.65	1.464	0.204	0.086
LP	2.79 – 3.61	3.168	0.399	0.168
WPB	3.10 – 4.13	3.562	0.511	0.216
WPT	3.10 – 4.33	3.818	0.583	0.246
WElM	3.92 – 5.78	4.984	0.894	0.377
LEl	6.09 – 9.49	7.565	1.503	0.634
B. Proportions.				
WPB/LP	1.03 – 1.17	1.123	0.055	0.023
WPT/WPB	1.00 – 1.13	1.066	0.062	0.026
WRA/LR	0.71 – 0.84	0.777	0.060	0.025
WRA/WF	0.82 – 0.94	0.887	0.057	0.024
WElM/LEl	0.61 – 0.71	0.660	0.047	0.020
LP/LEl	0.38 – 0.46	0.421	0.036	0.015

Table 12. Descriptive statistics for *A. jacobinus* based on eight males and eight females from Turlock, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.16 – 2.88	2.530	0.314	0.148
WF	1.76 – 2.24	2.070	0.226	0.107
WRA	1.52 – 1.92	1.770	0.175	0.082
LP	3.36 – 4.32	3.920	0.425	0.201
WPB	3.68 – 4.64	4.320	0.497	0.234
WPT	3.84 – 4.96	4.440	0.525	0.247
WElM	5.12 – 6.88	6.140	0.769	0.362
LEl	7.20 –10.24	9.000	1.325	0.625
B. Proportions.				
WPB/LP	1.07 – 1.16	1.102	0.044	0.021
WPT/WPB	0.97 – 1.07	1.028	0.047	0.022
WRA/LR	0.67 – 0.73	0.701	0.035	0.017
WRA/WF	0.79 – 0.89	0.856	0.056	0.026
WElM/LEl	0.65 – 0.71	0.684	0.032	0.015
LP/LEl	0.40 – 0.47	0.437	0.033	0.016
Females				
A. Measurements, in mm.				
LR	2.08 – 3.04	2.670	0.471	0.222
WF	1.84 – 2.48	2.150	0.336	0.158
WRA	1.60 – 2.08	1.840	0.213	0.100
LP	3.36 – 4.80	4.120	0.723	0.341
WPB	3.68 – 4.96	4.420	0.666	0.314
WPT	3.84 – 5.28	4.580	0.736	0.347
WElM	5.12 – 7.52	6.480	1.183	0.557
LEl	7.52 –10.88	9.600	1.702	0.802
B. Proportions.				
WPB/LP	1.03 – 1.13	1.075	0.055	0.026
WPT/WPB	1.00 – 1.07	1.036	0.039	0.018
WRA/LR	0.65 – 0.77	0.693	0.056	0.026
WRA/WF	0.79 – 0.92	0.859	0.058	0.027
WElM/LEl	0.66 – 0.69	0.675	0.014	0.006
LP/LEl	0.42 – 0.45	0.429	0.018	0.008

Table 13. Descriptive statistics for *A. albovestitus* based on eight males and eight females from Portal, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.24 – 3.04	2.600	0.449	0.212
WF	1.60 – 2.00	1.820	0.200	0.094
WRA	1.60 – 2.00	1.800	0.231	0.109
LP	3.52 – 4.80	4.280	0.688	0.324
WPB	3.68 – 5.28	4.520	0.756	0.356
WPT	3.60 – 4.80	4.290	0.608	0.287
WElM	5.28 – 7.36	6.440	1.087	0.512
LEl	8.48 –11.68	10.000	1.653	0.779
B. Proportions.				
WPB/LP	1.03 – 1.10	1.056	0.039	0.018
WPT/WPB	0.91 – 1.00	0.951	0.045	0.021
WRA/LR	0.63 – 0.75	0.695	0.061	0.029
WRA/WF	0.91 – 1.00	0.989	0.048	0.023
WElM/LEl	0.60 – 0.72	0.645	0.055	0.026
LP/LEl	0.40 – 0.45	0.428	0.024	0.011
Females				
A. Measurements, in mm.				
LR	2.24 – 3.36	2.770	0.559	0.263
WF	1.60 – 2.32	2.030	0.400	0.189
WRA	1.52 – 2.24	1.940	0.414	0.195
LP	3.68 – 5.12	4.550	0.820	0.387
WPB	3.84 – 5.60	4.780	1.012	0.477
WPT	3.84 – 5.44	4.640	0.907	0.428
WElM	5.60 – 8.16	6.840	1.450	0.683
LEl	8.48 –13.76	10.780	2.623	1.236
B. Proportions.				
WPB/LP	0.98 – 1.09	1.049	0.061	0.029
WPT/WPB	0.94 – 1.00	0.972	0.031	0.015
WRA/LR	0.67 – 0.74	0.700	0.047	0.022
WRA/WF	0.92 – 1.00	0.955	0.038	0.018
WElM/LEl	0.95 – 0.69	0.637	0.054	0.025
LP/LEl	0.37 – 0.46	0.425	0.039	0.018

Table 14. Descriptive statistics for *A. saginatus* based on eight males and eight females from 5 mi. SW. Patagonia, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.72 – 3.28	2.940	0.285	0.134
WF	1.84 – 2.16	1.980	0.154	0.072
WRA	1.76 – 2.16	1.950	0.212	0.100
LP	4.32 – 5.60	4.840	0.676	0.319
WPB	4.48 – 5.60	5.080	0.555	0.262
WPT	4.32 – 5.12	4.720	0.406	0.191
WEIM	6.56 – 7.84	7.280	0.691	0.326
LEl	11.04 – 13.12	12.060	1.133	0.534
B. Proportions.				
WPB/LP	1.00 – 1.11	1.052	0.062	0.029
WPT/WPB	0.88 – 0.97	0.930	0.044	0.021
WRA/LR	0.63 – 0.73	0.664	0.056	0.026
WRA/WF	0.92 – 1.08	0.985	0.079	0.037
WEIM/LEl	0.59 – 0.62	0.604	0.016	0.007
LP/LEl	0.38 – 0.43	0.401	0.024	0.011
Females				
A. Measurements, in mm.				
LR	2.96 – 3.60	3.156	0.288	0.128
WF	2.00 – 2.32	2.151	0.152	0.068
WRA	1.92 – 2.40	2.169	0.228	0.101
LP	4.96 – 5.92	5.351	0.418	0.186
WPB	4.96 – 6.08	5.511	0.525	0.233
WPT	4.64 – 5.76	5.156	0.573	0.255
WEIM	7.36 – 8.96	8.018	0.782	0.348
LEl	12.48 – 14.72	13.387	1.170	0.520
B. Proportions.				
WPB/LP	1.00 – 1.06	1.029	0.031	0.014
WPT/WPB	0.91 – 0.97	0.935	0.030	0.013
WRA/LR	0.63 – 0.74	0.688	0.056	0.025
WRA/WF	0.96 – 1.04	1.007	0.046	0.021
WEIM/LEl	0.56 – 0.64	0.599	0.030	0.013
LP/LEl	0.39 – 0.43	0.400	0.017	0.008

Table 15. Descriptive statistics for *C. erysimi* based on eight males and eight females from Redondo, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.68 – 2.16	1.925	0.279	0.131
WF	1.24 – 1.56	1.410	0.160	0.075
WRA	1.24 – 1.56	1.390	0.184	0.087
LP	3.04 – 3.68	3.400	0.454	0.214
WPB	2.96 – 4.16	3.510	0.603	0.284
WElH	3.28 – 4.64	3.930	0.721	0.340
WElM	3.60 – 4.96	4.300	0.780	0.367
LEl	7.04 – 9.60	8.480	1.405	0.662
LEy	0.92 – 1.20	1.060	0.143	0.068
WEy	0.56 – 0.68	0.625	0.078	0.037
B. Proportions.				
WEy/LEy	0.57 – 0.61	0.590	0.026	0.012
WPB/LP	0.97 – 1.13	1.031	0.077	0.036
WRA/LR	0.69 – 0.76	0.723	0.039	0.019
WRA/WF	0.94 – 1.05	0.986	0.054	0.026
WElM/LEl	0.49 – 0.53	0.507	0.021	0.010
LP/LEl	0.38 – 0.43	0.402	0.022	0.010
Females				
A. Measurements, in mm.				
LR	1.84 – 2.32	2.050	0.252	0.119
WF	1.28 – 1.60	1.420	0.154	0.072
WRA	1.20 – 1.36	1.310	0.095	0.045
LP	3.12 – 3.92	3.510	0.365	0.172
WPB	3.04 – 3.76	3.530	0.398	0.187
WElH	3.36 – 4.40	3.960	0.476	0.224
WElM	3.92 – 4.80	4.420	0.409	0.193
LEl	7.52 – 9.76	8.720	1.073	0.506
LEy	0.88 – 1.12	1.035	0.113	0.053
WEy	0.52 – 0.72	0.640	0.101	0.048
B. Proportions.				
WEy/LEy	0.58 – 0.67	0.618	0.047	0.022
WPB/LP	0.96 – 1.07	1.006	0.057	0.027
WRA/LR	0.57 – 0.68	0.641	0.054	0.026
WRA/WF	0.85 – 1.03	0.925	0.074	0.035
WElM/LEl	0.49 – 0.53	0.508	0.020	0.009
LP/LEl	0.38 – 0.42	0.403	0.023	0.011

Table 16. Descriptive statistics for *C. eustictorrhinus* based on 13 males and 14 females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.80 – 2.20	2.000	0.171	0.063
WF	0.96 – 1.48	1.329	0.238	0.088
WRA	1.08 – 1.40	1.255	0.142	0.052
LP	2.64 – 3.60	3.360	0.421	0.156
WPB	2.80 – 3.92	3.502	0.439	0.162
WElH	3.44 – 4.64	4.148	0.547	0.203
WElM	3.68 – 4.96	4.437	0.558	0.206
LEl	6.88 – 9.44	8.369	1.057	0.391
LEy	0.96 – 1.16	1.068	0.096	0.036
WEy	0.52 – 0.72	0.637	0.075	0.028
B. Proportions.				
WEy/LEy	0.54 – 0.67	0.597	0.062	0.023
WPB/LP	1.02 – 1.09	1.043	0.029	0.011
WRA/LR	0.59 – 0.69	0.627	0.038	0.014
WRA/WF	0.88 – 1.13	0.952	0.116	0.043
WElM/LEl	0.49 – 0.56	0.530	0.028	0.010
LP/LEl	0.38 – 0.43	0.402	0.026	0.010
Females				
A. Measurements, in mm.				
LR	1.80 – 2.20	2.011	0.200	0.071
WF	1.08 – 1.52	1.331	0.170	0.061
WRA	1.12 – 1.36	1.214	0.109	0.039
LP	2.88 – 3.76	3.406	0.329	0.117
WPB	3.12 – 4.00	3.543	0.422	0.151
WElH	3.60 – 4.64	4.126	0.509	0.181
WElM	3.92 – 5.04	4.423	0.497	0.177
LEl	0.75 – 9.44	8.434	0.962	0.343
LEy	1.00 – 1.20	1.089	0.113	0.040
WEy	0.56 – 0.68	0.620	0.056	0.020
B. Proportions.				
WEy/LEy	0.52 – 0.64	0.571	0.056	0.020
WPB/LP	0.98 – 1.14	1.040	0.059	0.021
WRA/LR	0.56 – 0.65	0.604	0.033	0.012
WRA/WF	0.87 – 1.11	0.916	0.092	0.033
WElM/LEl	0.49 – 0.55	0.525	0.024	0.009
LP/LEl	0.38 – 0.43	0.404	0.026	0.009

Table 17. Descriptive statistics for *C. pleuralis* based on eight males and eight females from Palm Springs, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.72 – 1.96	1.840	0.140	0.066
WF	0.96 – 1.12	1.040	0.096	0.045
WRA	0.80 – 1.00	0.935	0.090	0.043
LP	2.72 – 3.04	2.900	0.154	0.072
WPB	2.40 – 3.04	2.800	0.308	0.145
WElH	3.04 – 3.68	3.460	0.378	0.178
WElM	3.20 – 3.60	3.430	0.235	0.111
LEl	7.44 – 8.72	8.040	0.700	0.330
LEy	0.84 – 1.00	0.955	0.081	0.038
WEy	0.44 – 0.56	0.495	0.064	0.030
B. Proportions.				
WEy/LEy	0.46 – 0.58	0.519	0.068	0.032
WPB/LP	0.88 – 1.03	0.965	0.065	0.031
WRA/LR	0.47 – 0.56	0.509	0.049	0.023
WRA/WF	0.83 – 1.00	0.900	0.086	0.041
WElM/LEl	0.40 – 0.46	0.427	0.031	0.014
LP/LEl	0.35 – 0.38	0.361	0.023	0.011
Females				
A. Measurements, in mm.				
LR	1.48 – 1.92	1.710	0.258	0.122
WF	0.88 – 1.08	0.990	0.110	0.052
WRA	0.72 – 1.00	0.865	0.140	0.066
LP	2.40 – 3.04	2.720	0.385	0.181
WPB	2.24 – 3.04	2.650	0.442	0.208
WElH	2.80 – 3.68	3.230	0.540	0.255
WElM	2.72 – 3.68	3.110	0.546	0.257
LEl	5.76 – 8.96	7.410	1.556	0.733
LEy	0.76 – 1.00	0.915	0.122	0.057
WEy	0.40 – 0.56	0.485	0.081	0.038
B. Proportions.				
WEy/LEy	0.46 – 0.57	0.530	0.053	0.025
WPB/LP	0.93 – 1.03	0.973	0.060	0.029
WRA/LR	0.46 – 0.53	0.506	0.040	0.019
WRA/WF	0.78 – 0.93	0.873	0.078	0.037
WElM/LEl	0.39 – 0.47	0.422	0.038	0.018
LP/LEl	0.33 – 0.42	0.370	0.043	0.020

Table 18. Descriptive statistics for *C. subcylindricus* based on seven males and 17 females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.68 – 2.08	1.937	0.227	0.114
WF	1.00 – 1.16	1.051	0.102	0.052
WRA	1.12 – 1.36	1.217	0.124	0.062
LP	2.96 – 3.52	3.291	0.313	0.158
WPB	2.88 – 3.68	3.303	0.431	0.217
WElH	3.52 – 4.32	3.943	0.425	0.214
WElM	3.68 – 4.64	4.206	0.571	0.288
LEl	7.68 – 9.44	8.663	1.077	0.543
LEy	0.92 – 1.12	1.034	0.117	0.059
WEy	0.56 – 0.68	0.617	0.068	0.034
B. Proportions.				
WEy/LEy	0.57 – 0.64	0.597	0.036	0.018
WPB/LP	0.95 – 1.05	1.002	0.053	0.027
WRA/LR	0.58 – 0.69	0.630	0.054	0.027
WRA/WF	1.07 – 1.24	1.158	0.081	0.041
WElM/LEl	0.45 – 0.50	0.485	0.028	0.014
LP/LEl	0.36 – 0.40	0.381	0.019	0.010
Females				
A. Measurements, in mm.				
LR	1.68 – 2.28	2.049	0.281	0.091
WF	0.92 – 1.40	1.118	0.168	0.054
WRA	1.12 – 1.40	1.266	0.134	0.043
LP	2.80 – 3.92	3.426	0.515	0.166
WPB	2.80 – 4.00	3.449	0.502	0.162
WElH	3.28 – 4.72	4.061	0.643	0.208
WElM	3.52 – 5.12	4.348	0.766	0.248
LEl	7.52 – 10.24	8.951	1.210	0.391
LEy	0.88 – 1.16	1.052	0.123	0.040
WEy	0.52 – 0.76	0.609	0.084	0.027
B. Proportions.				
WEy/LEy	0.52 – 0.68	0.580	0.065	0.021
WPB/LP	0.96 – 1.07	1.008	0.052	0.017
WRA/LR	0.56 – 0.69	0.619	0.042	0.013
WRA/WF	1.00 – 1.26	1.137	0.087	0.028
WElM/LEl	0.43 – 0.53	0.485	0.039	0.013
LP/LEl	0.36 – 0.41	0.383	0.022	0.007

Table 19. Descriptive statistics for *C. longinasus* based on 10 males and 10 females from
              Hemet Reservoir, Herkey Creek, and Idyllwild, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.80 – 2.28	1.980	0.283	0.119
WF	1.04 – 1.24	1.112	0.089	0.037
WRA	0.84 – 1.08	0.952	0.101	0.043
LP	2.56 – 3.44	2.976	0.434	0.183
WPB	2.72 – 3.44	3.056	0.298	0.126
WElH	3.20 – 4.00	3.560	0.345	0.145
WElM	3.52 – 4.40	3.936	0.466	0.196
LEl	6.72 – 8.64	7.744	0.934	0.394
LEy	0.92 – 1.04	0.960	0.063	0.027
WEy	0.52 – 0.64	0.556	0.066	0.028
B. Proportions.				
WEy/LEy	0.52 – 0.65	0.579	0.060	0.025
WPB/LP	0.97 – 1.13	1.030	0.071	0.030
WRA/LR	0.40 – 0.56	0.485	0.080	0.034
WRA/WF	0.74 – 0.93	0.858	0.130	0.043
WElM/LEl	0.48 – 0.54	0.509	0.031	0.013
LP/LEl	0.36 – 0.40	0.384	0.023	0.010
Females				
A. Measurements, in mm.				
LR	1.92 – 2.52	2.296	0.261	0.110
WF	1.08 – 1.20	1.172	0.064	0.027
WRA	0.80 – 1.00	0.888	0.093	0.039
LP	2.96 – 3.44	3.184	0.232	0.098
WPB	2.96 – 3.36	3.264	0.202	0.085
WElH	3.36 – 4.08	3.824	0.329	0.139
WElM	3.84 – 4.64	4.272	0.432	0.182
LEl	7.52 – 8.80	8.224	0.744	0.313
LEy	0.92 – 1.08	0.984	0.064	0.027
WEy	0.52 – 0.60	0.564	0.034	0.014
B. Proportions.				
WEy/LEy	0.52 – 0.63	0.574	0.048	0.020
WPB/LP	0.95 – 1.11	1.027	0.081	0.034
WRA/LR	0.34 – 0.44	0.388	0.043	0.018
WRA/WF	0.70 – 0.83	0.758	0.069	0.029
WElM/LEl	0.48 – 0.58	0.520	0.043	0.018
LP/LEl	0.37 – 0.40	0.388	0.015	0.006

Table 20. Descriptive statistics for *C. texanus* based on eight males and eight females from Mile 19, Hitchcock Highway, Santa Catalina Mountains, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.44 – 1.64	1.535	0.101	0.048
WF	0.84 – 0.96	0.900	0.064	0.030
WRA	0.80 – 0.88	0.830	0.042	0.020
LP	2.16 – 2.56	2.320	0.192	0.090
WPB	2.48 – 2.56	2.510	0.062	0.029
WElH	2.88 – 3.20	3.030	0.175	0.082
WElM	3.12 – 3.36	3.230	0.156	0.052
LEl	6.32 – 6.96	6.580	0.325	0.153
LEy	0.80 – 0.88	0.825	0.045	0.021
WEy	0.44 – 0.52	0.475	0.038	0.018
B. Proportions.				
WEy/LEy	0.52 – 0.62	0.576	0.051	0.024
WPB/LP	1.00 – 1.15	1.084	0.072	0.034
WRA/LR	0.51 – 0.56	0.541	0.025	0.012
WRA/WF	0.87 – 1.00	0.924	0.073	0.034
WElM/LEl	0.47 – 0.51	0.491	0.021	0.010
LP/LEl	0.34 – 0.38	0.353	0.023	0.011
Females				
A. Measurements, in mm.				
LR	1.32 – 1.72	1.515	0.199	0.094
WF	0.84 – 1.00	0.905	0.078	0.026
WRA	0.68 – 0.80	0.740	0.064	0.030
LP	2.00 – 2.56	2.360	0.301	0.142
WPB	2.24 – 2.72	2.530	0.231	0.109
WElH	2.56 – 3.20	2.990	0.307	0.145
WElM	2.72 – 3.44	3.210	0.336	0.158
LEl	5.52 – 7.04	6.530	0.748	0.352
LEy	0.76 – 0.92	0.830	0.077	0.036
WEy	0.44 – 0.52	0.480	0.056	0.026
B. Proportions.				
WEy/LEy	0.55 – 0.62	0.578	0.036	0.017
WPB/LP	1.00 – 1.12	1.075	0.063	0.030
WRA/LR	0.46 – 0.55	0.490	0.045	0.021
WRA/WF	0.77 – 0.87	0.818	0.048	0.023
WElM/LEl	0.48 – 0.51	0.492	0.017	0.008
LP/LEl	0.34 – 0.38	0.361	0.016	0.008

Table 21. Descriptive statistics for *C. americanus* based on eight males and eight females from Mercy Hot Springs, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.28 – 2.44	1.815	0.555	0.262
WF	0.88 – 1.44	1.155	0.261	0.123
WRA	0.80 – 1.24	1.005	0.234	0.111
LP	1.84 – 3.60	2.670	0.836	0.394
WPB	1.92 – 3.60	2.760	0.831	0.392
WElH	2.40 – 4.56	3.390	1.058	0.499
WElM	2.88 – 4.88	3.700	0.985	0.464
LEl	4.80 – 9.28	6.980	2.135	1.007
LEy	0.72 – 1.16	0.950	0.239	0.113
WEy	0.40 – 0.72	0.570	0.156	0.073
B. Proportions.				
WEy/LEy	0.54 – 0.65	0.600	0.053	0.025
WPB/LP	1.00 – 1.09	1.035	0.044	0.021
WRA/LR	0.51 – 0.63	0.559	0.052	0.025
WRA/WF	0.81 – 0.91	0.870	0.049	0.023
WElM/LEl	0.50 – 0.60	0.534	0.044	0.021
LP/LEl	0.37 – 0.40	0.383	0.013	0.006
Females				
A. Measurements, in mm.				
LR	1.36 – 2.44	1.755	0.504	0.238
WF	0.88 – 1.52	1.130	0.294	0.138
WRA	0.72 – 1.28	0.910	0.260	0.123
LP	2.00 – 3.44	2.480	0.669	0.316
WPB	1.92 – 3.68	2.610	0.806	0.380
WElH	2.40 – 4.48	3.180	0.931	0.439
WElM	2.72 – 4.88	3.540	0.981	0.462
LEl	4.96 – 8.96	6.560	1.796	0.846
LEy	0.72 – 1.28	0.925	0.251	0.118
WEy	0.40 – 0.72	0.540	0.136	0.064
B. Proportions.				
WEy/LEy	0.53 – 0.67	0.586	0.064	0.030
WPB/LP	0.96 – 1.10	1.048	0.073	0.034
WRA/LR	0.43 – 0.59	0.521	0.065	0.031
WRA/WF	0.70 – 0.91	0.806	0.094	0.044
WElM/LEl	0.50 – 0.56	0.540	0.029	0.013
LP/LEl	0.36 – 0.40	0.379	0.020	0.009

Table 22. Descriptive statistics for *C. frontalis* based on eight males and eight females from Medicine Hat, Alberta

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.52 – 2.00	1.745	0.231	0.109
WF	1.00 – 1.28	1.145	0.150	0.071
WRA	0.92 – 1.20	1.070	0.163	0.077
LP	2.32 – 3.04	2.710	0.376	0.177
WPB	2.64 – 3.44	3.030	0.437	0.206
WElH	3.20 – 4.16	3.650	0.544	0.256
WElM	3.52 – 4.56	4.020	0.634	0.299
LEl	6.40 – 8.80	7.540	1.279	0.603
LEy	0.80 – 1.00	0.925	0.130	0.061
WEy	0.52 – 0.64	0.565	0.075	0.035
B. Proportions				
WEy/LEy	0.54 – 0.65	0.612	0.055	0.026
WPB/LP	1.09 – 1.14	1.118	0.028	0.013
WRA/LR	0.56 – 0.71	0.614	0.064	0.030
WRA/WF	0.89 – 0.97	0.934	0.037	0.017
WElM/LEl	0.50 – 0.55	0.534	0.029	0.014
LP/LEl	0.35 – 0.38	0.360	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.52 – 2.04	1.785	0.264	0.125
WF	1.00 – 1.36	1.170	0.183	0.087
WRA	0.96 – 1.12	1.055	0.078	0.037
LP	2.40 – 3.12	2.880	0.406	0.191
WPB	2.64 – 3.60	3.140	0.424	0.200
WElH	3.20 – 4.40	3.830	0.542	0.256
WElM	3.52 – 4.88	4.220	0.601	0.283
LEl	6.56 – 8.48	7.740	1.034	0.487
LEy	0.80 – 1.12	1.000	0.150	0.071
WEy	0.48 – 0.60	0.570	0.070	0.033
B. Proportions.				
WEy/LEy	0.52 – 0.60	0.572	0.052	0.025
WPB/LP	1.03 – 1.16	1.092	0.074	0.035
WRA/LR	0.55 – 0.65	0.594	0.055	0.026
WRA/WF	0.82 – 1.00	0.907	0.090	0.042
WElM/LEl	0.52 – 0.58	0.545	0.030	0.014
LP/LEl	0.36 – 0.39	0.372	0.016	0.007

Table 23. Descriptive statistics for *C. canescens* based on eight males and eight females from Denver, Colorado

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.48 – 2.00	1.860	0.246	0.116
WF	1.28 – 1.64	1.510	0.156	0.074
WRA	1.24 – 1.60	1.495	0.163	0.077
LP	2.24 – 3.20	2.820	0.419	0.198
WPB	2.64 – 3.76	3.370	0.507	0.239
WElH	3.12 – 4.24	3.870	0.497	0.234
WElM	3.28 – 4.64	4.190	0.608	0.287
LEl	5.60 – 7.76	7.100	1.086	0.512
LEy	0.80 – 1.00	0.965	0.104	0.049
WEy	0.56 – 0.72	0.645	0.075	0.035
B. Proportions				
WEy/LEy	0.63 – 0.72	0.669	0.049	0.023
WPB/LP	1.16 – 1.25	1.195	0.046	0.022
WRA/LR	0.77 – 0.84	0.805	0.037	0.017
WRA/WF	0.97 – 1.03	0.990	0.037	0.017
WElM/LEl	0.57 – 0.61	0.591	0.022	0.010
LP/LEl	0.38 – 0.42	0.398	0.023	0.011
Females				
A. Measurements, in mm.				
LR	1.52 – 2.04	1.880	0.276	0.130
WF	1.28 – 1.72	1.565	0.199	0.094
WRA	1.32 – 1.72	1.545	0.195	0.092
LP	2.40 – 3.12	2.880	0.357	0.168
WPB	2.72 – 3.84	3.390	0.517	0.244
WElH	3.20 – 4.40	3.940	0.614	0.290
WElM	3.36 – 4.88	4.300	0.740	0.348
LEl	5.76 – 8.00	7.220	1.220	0.575
LEy	0.88 – 1.08	0.985	0.124	0.058
WEy	0.56 – 0.72	0.660	0.085	0.040
B. Proportions				
WEy/LEy	0.62 – 0.73	0.671	0.061	0.029
WPB/LP	1.13 – 1.23	1.176	0.052	0.025
WRA/LR	0.76 – 0.87	0.824	0.054	0.025
WRA/WF	0.95 – 1.03	0.988	0.048	0.022
WElM/LEl	0.57 – 0.62	0.596	0.028	0.013
LP/LEl	0.38 – 0.43	0.400	0.026	0.012

Table 24. Descriptive statistics for *C. infrequens* based on two males and six females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.64 – 1.72	1.68	–	–
WF	1.24 – 1.24	1.24	–	–
WRA	1.28 – 1.36	1.32	–	–
LP	2.96 – 3.20	3.08	–	–
WPB	2.96 – 3.44	3.20	–	–
WElH	3.52 – 3.92	3.72	–	–
WElM	4.08 – 4.16	4.12	–	–
LEl	6.88 – 7.36	7.12	–	–
LEy	0.88 – 1.00	0.94	–	–
WEy	0.52 – 0.60	0.56	–	–
B. Proportions				
WEy/LEy	0.59 – 0.60	0.60	–	–
WPB/LP	1.00 – 1.08	1.04	–	–
WRA/LR	0.78 – 0.79	0.79	–	–
WRA/WF	1.03 – 1.10	1.07	–	–
WElM/LEl	0.55 – 0.61	0.58	–	–
LP/LEl	0.43 – 0.44	0.43	–	–
Females				
A. Measurements, in mm.				
LR	1.44 – 1.88	1.667	0.239	0.130
WF	1.24 – 1.40	1.327	0.080	0.043
WRA	1.32 – 1.44	1.373	0.090	0.049
LP	3.04 – 3.52	3.267	0.308	0.167
WPB	3.12 – 3.60	3.373	0.278	0.151
WElH	3.60 – 4.32	4.040	0.460	0.251
WElM	3.76 – 4.72	4.400	0.563	0.307
LEl	7.20 – 8.48	7.840	0.759	0.413
LEy	0.96 – 1.16	1.067	0.105	0.057
WEy	0.52 – 0.60	0.573	0.049	0.027
B. Proportions.				
WEy/LEy	0.52 – 0.58	0.538	0.032	0.018
WPB/LP	1.00 – 1.05	1.033	0.031	0.017
WRA/LR	0.75 – 0.92	0.828	0.088	0.048
WRA/WF	1.00 – 1.09	1.036	0.061	0.033
WElM/LEl	0.52 – 0.60	0.561	0.046	0.025
LP/LEl	0.40 – 0.45	0.417	0.027	0.015

Table 25. Descriptive statistics for *C. puberulus* based on six males and 10 females from Colorado Springs, Colorado

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm				
LR	1.44 – 1.64	1.513	0.128	0.070
WF	1.24 – 1.40	1.313	0.110	0.060
WRA	1.16 – 1.28	1.213	0.082	0.045
LP	2.48 – 3.04	2.627	0.317	0.173
WPB	2.64 – 2.96	2.760	0.197	0.107
WElH	3.04 – 3.44	3.200	0.201	0.109
WElM	3.36 – 3.60	3.493	0.145	0.079
LEl	5.76 – 6.48	6.067	0.425	0.232
LEy	0.84 – 1.04	0.900	0.106	0.058
WEy	0.52 – 0.56	0.533	0.031	0.017
B. Proportions.				
WEy/LEy	0.50 – 0.67	0.600	0.085	0.046
WPB/LP	0.97 – 1.13	1.054	0.086	0.047
WRA/LR	0.71 – 0.87	0.804	0.083	0.045
WRA/WF	0.86 – 1.00	0.926	0.080	0.044
WElM/LEl	0.53 – 0.61	0.577	0.039	0.021
LP/LEl	0.40 – 0.47	0.433	0.033	0.018
Females				
A. Measurements, in mm.				
LR	1.28 – 1.76	1.548	0.255	0.107
WF	1.20 – 1.48	1.356	0.161	0.068
WRA	1.00 – 1.36	1.196	0.178	0.075
LP	2.24 – 3.04	2.648	0.454	0.192
WPB	2.24 – 3.36	2.792	0.520	0.219
WElH	2.64 – 3.84	3.280	0.640	0.270
WElM	2.96 – 4.08	3.608	0.597	0.252
LEl	4.96 – 7.52	6.328	1.253	0.529
LEy	0.76 – 1.04	0.916	0.159	0.067
WEy	0.48 – 0.60	0.552	0.079	0.033
B. Proportions.				
WEy/LEy	0.58 – 0.63	0.604	0.035	0.015
WPB/LP	0.97 – 1.11	1.054	0.067	0.028
WRA/LR	0.74 – 0.82	0.774	0.037	0.015
WRA/WF	0.83 – 0.94	0.881	0.050	0.021
WElM/LEl	0.54 – 0.60	0.572	0.031	0.013
LP/LEl	0.40 – 0.45	0.420	0.021	0.009

Table 26. Descriptive statistics for *C. collaris* based on seven males and six females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.60 – 2.20	1.971	0.333	0.168
WF	1.24 – 1.72	1.486	0.248	0.125
WRA	1.16 – 1.44	1.280	0.162	0.082
LP	2.72 – 3.84	3.211	0.633	0.319
WPB	3.04 – 4.24	3.611	0.673	0.339
WElH	3.68 – 5.20	4.446	0.840	0.423
WElM	4.24 – 5.60	4.937	0.758	0.382
LEl	6.72 – 9.12	7.909	1.412	0.712
LEy	0.88 – 1.24	1.011	0.176	0.089
WEy	0.56 – 0.72	0.629	0.090	0.045
B. Proportions.				
WEy/LEy				
WPB/LP	1.07 – 1.21	1.126	0.075	0.038
WRA/LR	0.61 – 0.73	0.652	0.062	0.031
WRA/WF	0.83 – 0.94	0.864	0.065	0.033
WElM/LEl	0.59 – 0.64	0.625	0.028	0.014
LP/LEl	0.40 – 0.42	0.406	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.68 – 2.24	1.940	0.321	0.175
WF	1.32 – 1.72	1.513	0.219	0.119
WRA	1.16 – 1.36	1.240	0.126	0.069
LP	2.80 – 3.68	3.173	0.561	0.306
WPB	3.28 – 4.16	3.747	0.534	0.291
WElH	3.84 – 5.12	4.507	0.798	0.435
WElM	4.40 – 5.76	5.080	0.861	0.469
LEl	7.20 – 8.96	8.133	1.034	0.563
LEy	1.00 – 1.08	1.053	0.049	0.027
WEy	0.56 – 0.72	0.633	0.110	0.060
B. Proportions.				
WEy/LEy	0.52 – 0.67	0.601	0.094	0.051
WPB/LP	1.13 – 1.24	1.183	0.060	0.033
WRA/LR	0.61 – 0.69	0.642	0.051	0.028
WRA/WF	0.79 – 0.88	0.822	0.058	0.031
WElM/LEl	0.60 – 0.65	0.623	0.028	0.015
LP/LEl	0.37 – 0.41	0.390	0.025	0.014

Table 27. Descriptive statistics for *C. notolomus* based on 11 males and 13 females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.56 – 2.24	2.015	0.298	0.120
WF	1.20 – 1.52	1.407	0.144	0.058
WRA	1.16 – 1.40	1.313	0.096	0.039
LP	2.48 – 3.68	3.389	0.518	0.208
WPB	2.88 – 4.00	3.615	0.425	0.171
WElH	3.36 – 4.64	4.327	0.541	0.217
WElM	3.68 – 5.20	4.822	0.666	0.268
LEl	5.92 – 9.12	8.044	1.337	0.537
LEy	0.96 – 1.16	1.058	0.102	0.041
WEy	0.56 – 0.72	0.636	0.068	0.027
B. Proportions				
WEy/LEy	0.55 – 0.65	0.602	0.057	0.023
WPB/LP	1.02 – 1.16	1.070	0.061	0.025
WRA/LR	0.60 – 0.77	0.656	0.081	0.033
WRA/WF	0.84 – 0.97	0.935	0.057	0.023
WElM/LEl	0.56 – 0.64	0.601	0.038	0.015
LP/LEl	0.40 – 0.44	0.422	0.024	0.010
Females				
A. Measurements, in mm.				
LR	1.80 – 2.32	2.059	0.242	0.090
WF	1.24 – 1.60	1.437	0.177	0.066
WRA	1.16 – 1.48	1.302	0.162	0.060
LP	3.12 – 4.16	3.575	0.466	0.172
WPB	3.20 – 4.40	3.809	0.555	0.206
WElH	3.76 – 5.12	4.517	0.675	0.250
WElM	4.24 – 5.92	5.083	0.760	0.281
LEl	7.04 – 9.44	8.455	1.159	0.429
LEy	0.96 – 1.20	1.083	0.119	0.044
WEy	0.56 – 0.72	0.646	0.073	0.027
B. Proportions				
WEy/LEy	0.54 – 0.65	0.597	0.051	0.019
WPB/LP	1.00 – 1.12	1.065	0.051	0.019
WRA/LR	0.59 – 0.68	0.633	0.049	0.018
WRA/WF	0.85 – 0.95	0.906	0.042	0.015
WElM/LEl	0.58 – 0.64	0.601	0.030	0.011
LP/LEl	0.40 – 0.45	0.423	0.022	0.008

Table 28. Descriptive statistics for *C. poricollis* based on eight males and eight females from 1mi. N. Little Lake, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.52 – 1.88	1.700	0.195	0.092
WF	0.88 – 1.08	0.950	0.131	0.062
WRA	0.96 – 1.12	1.045	0.087	0.041
LP	2.24 – 2.72	2.500	0.238	0.112
WPB	2.48 – 3.04	2.730	0.268	0.126
WElH	2.96 – 3.68	3.320	0.345	0.163
WElM	3.20 – 3.76	3.530	0.311	0.146
LEl	6.40 – 7.36	6.880	0.602	0.284
LEy	0.84 – 1.00	0.920	0.072	0.034
WEy	0.44 – 0.52	0.475	0.038	0.018
B. Proportions				
WEy/LEy	0.48 – 0.55	0.517	0.038	0.018
WPB/LP	1.03 – 1.15	1.093	0.061	0.029
WRA/LR	0.59 – 0.68	0.616	0.049	0.023
WRA/WF	1.00 – 1.18	1.104	0.083	0.039
WElM/LEl	0.50 – 0.53	0.513	0.015	0.007
LP/LEl	0.34 – 0.39	0.364	0.027	0.013
Females				
A. Measurements, in mm.				
LR	1.52 – 1.92	1.735	0.208	0.098
WF	0.88 – 1.12	0.980	0.120	0.057
WRA	1.00 – 1.24	1.075	0.122	0.057
LP	2.24 – 2.96	2.530	0.345	0.163
WPB	2.56 – 3.28	2.860	0.394	0.186
WElH	2.96 – 4.16	3.430	0.582	0.274
WElM	3.36 – 4.56	3.750	0.600	0.283
LEl	6.40 – 8.64	7.260	1.096	0.516
LEy	0.84 – 1.04	0.940	0.091	0.043
WEy	0.44 – 0.56	0.500	0.072	0.034
B. Proportions.				
WEy/LEy	0.50 – 0.58	0.532	0.047	0.022
WPB/LP	1.09 – 1.25	1.132	0.079	0.037
WRA/LR	0.57 – 0.71	0.621	0.070	0.033
WRA/WF	1.04 – 1.14	1.098	0.059	0.028
WElM/LEl	0.50 – 0.53	0.516	0.015	0.007
LP/LEl	0.32 – 0.36	0.349	0.024	0.011

Table 29. Descriptive statistics for *C. calandroides* based on eight males and eight females from Hampton, New Hampshire

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.60 – 1.96	1.850	0.166	0.078
WF	1.08 – 1.24	1.180	0.085	0.040
WRA	1.08 – 1.24	1.170	0.089	0.042
LP	2.56 – 3.12	2.960	0.280	0.132
WPB	2.80 – 3.44	3.180	0.338	0.159
WElH	3.20 – 4.08	3.740	0.399	0.188
WElM	3.68 – 4.56	4.210	0.430	0.203
LEl	6.40 – 7.84	7.240	0.638	0.301
LEy	0.84 – 0.96	0.910	0.053	0.025
WEy	0.44 – 0.52	0.485	0.038	0.018
B. Proportions				
WEy/LEy	0.52 – 0.57	0.533	0.024	0.011
WPB/LP	1.00 – 1.13	1.075	0.064	0.030
WRA/LR	0.60 – 0.68	0.633	0.044	0.021
WRA/WF	0.94 – 1.04	0.992	0.053	0.025
WElM/LEl	0.57 – 0.60	0.581	0.016	0.007
LP/LEl	0.39 – 0.43	0.409	0.021	0.010
Females				
A. Measurements, in mm.				
LR	1.92 – 2.08	1.975	0.078	0.037
WF	1.20 – 1.28	1.235	0.050	0.024
WRA	1.12 – 1.28	1.190	0.077	0.036
LP	3.04 – 3.20	3.100	0.085	0.040
WPB	3.20 – 3.60	3.370	0.197	0.093
WElH	3.84 – 4.24	4.030	0.202	0.095
WElM	4.24 – 4.72	4.510	0.256	0.121
LEl	7.36 – 8.16	7.820	0.394	0.186
LEy	0.88 – 1.08	0.955	0.093	0.044
WEy	0.48 – 0.56	0.530	0.042	0.020
B. Proportions				
WEy/LEy	0.52 – 0.64	0.556	0.055	0.026
WPB/LP	1.03 – 1.18	1.087	0.070	0.033
WRA/LR	0.56 – 0.65	0.603	0.046	0.021
WRA/WF	0.93 – 1.00	0.964	0.040	0.019
WElM/LEl	0.55 – 0.63	0.577	0.038	0.018
LP/LEl	0.38 – 0.41	0.397	0.015	0.007

Table 30. Descriptive statistics for *C. boucardi* based on eight males and eight females from north of Tepatitlan, Jalisco, México

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.80 – 2.52	2.065	0.386	0.182
WF	1.08 – 1.48	1.280	0.190	0.089
WRA	1.08 – 1.68	1.315	0.307	0.145
LP	2.96 – 4.40	3.570	0.714	0.337
WPB	3.12 – 4.80	3.810	0.791	0.373
WElH	3.76 – 5.68	4.550	0.972	0.458
WElM	4.24 – 6.16	5.040	0.981	0.462
LEl	7.20 –10.72	8.62	1.900	0.896
LEy	0.96 – 1.32	1.095	0.192	0.091
WEy	0.60 – 0.76	0.665	0.106	0.050
B. Proportions				
WEy/LEy	0.58 – 0.64	0.608	0.036	0.017
WPB/LP	1.04 – 1.09	1.067	0.022	0.010
WRA/LR	0.57 – 0.67	0.635	0.051	0.024
WRA/WF	0.87 – 1.14	1.024	0.113	0.053
WElM/LEl	0.57 – 0.62	0.586	0.024	0.011
LP/LEl	0.40 – 0.44	0.415	0.018	0.009
Females				
A. Measurements, in mm.				
LR	1.52 – 2.40	2.115	0.501	0.236
WF	0.96 – 1.52	1.320	0.308	0.145
WRA	1.00 – 1.48	1.320	0.264	0.125
LP	2.56 – 4.16	3.560	0.846	0.399
WPB	2.48 – 4.56	3.760	1.073	0.506
WElH	3.04 – 5.44	4.550	1.284	0.605
WElM	3.68 – 5.76	5.03	1.177	0.555
LEl	6.08 –10.72	9.020	2.461	1.160
LEy	0.84 – 1.32	1.105	0.217	0.102
WEy	0.56 – 0.80	0.650	0.110	0.052
B. Proportions				
WEy/LEy	0.54 – 0.67	0.591	0.061	0.029
WPB/LP	0.97 – 1.13	1.051	0.075	0.036
WRA/LR	0.59 – 0.66	0.627	0.031	0.014
WRA/WF	0.95 – 1.06	1.004	0.068	0.032
WElM/LEl	0.54 – 0.61	0.560	0.032	0.015
LP/LEl	0.38 – 0.42	0.397	0.021	0.010

Table 31. Descriptive statistics for *C. trivittatus* based on eight males eight females from Albuquerque, New México

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.32 – 2.72	2.565	0.253	0.119
WF	1.60 – 1.88	1.740	0.190	0.089
WRA	1.44 – 1.76	1.585	0.178	0.084
LP	3.92 – 4.72	4.270	0.374	0.176
WPB	4.32 – 5.52	4.670	0.577	0.272
WEIH	4.80 – 6.08	5.330	0.608	0.287
WEIM	5.44 – 6.64	5.900	0.604	0.285
LEl	9.28 –11.68	10.400	1.126	0.531
LEy	1.08 – 1.52	1.270	0.212	0.100
WEy	0.60 – 0.84	0.735	0.120	0.056
B. Proportions				
WEy/LEy	0.55 – 0.63	0.579	0.035	0.017
WPB/LP	1.06 – 1.17	1.093	0.055	0.026
WRA/LR	0.58 – 0.65	0.618	0.031	0.015
WRA/WF	0.87 – 0.98	0.911	0.051	0.024
WEIM/LEl	0.55 – 0.59	0.568	0.018	0.009
LP/LEl	0.39 – 0.42	0.411	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.92 – 2.96	2.450	0.495	0.350
WF	1.32 – 1.84	1.670	0.279	0.132
WRA	1.16 – 1.68	1.500	0.246	0.116
LP	3.28 – 4.56	4.120	0.714	0.337
WPB	3.36 – 5.04	4.440	0.889	0.419
WEIH	3.76 – 6.16	5.170	1.202	0.566
WEIM	4.32 – 6.64	5.700	1.191	0.561
LEl	7.68 –11.20	9.940	1.789	0.843
LEy	0.96 – 1.44	1.225	0.231	0.109
WEy	0.56 – 0.80	0.710	0.119	0.056
B. Proportions				
WEy/LEy	0.56 – 0.61	0.581	0.030	0.014
WPB/LP	1.02 – 1.12	1.076	0.047	0.022
WRA/LR	0.57 – 0.68	0.615	0.061	0.029
WRA/WF	0.86 – 0.95	0.899	0.040	0.019
WEIM/LEl	0.55 – 0.59	0.572	0.024	0.011
LP/LEl	0.41 – 0.43	0.415	0.016	0.007

Table 32. Descriptive statistics for *C. placidus* based on 10 males and eight females from Panoche, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.40 – 2.80	2.592	0.240	0.101
WF	1.56 – 1.84	1.692	0.174	0.074
WRA	1.48 – 1.72	1.596	0.134	0.057
LP	3.60 – 4.32	4.008	0.364	0.154
WPB	4.00 – 4.88	4.408	0.465	0.196
WEIH	4.80 – 5.76	5.304	0.463	0.195
WEIM	5.20 – 6.48	5.776	0.699	0.295
LEl	9.92 –11.68	10.800	1.104	0.466
LEy	1.28 – 1.48	1.364	0.125	0.053
WEy	0.72 – 0.84	0.764	0.052	0.022
B. Proportions				
WEy/LEy	0.53 – 0.59	0.561	0.032	0.013
WPB/LP	1.04 – 1.18	1.100	0.072	0.030
WRA/LR	0.59 – 0.65	0.616	0.022	0.009
WRA/WF	0.91 – 1.00	0.945	0.048	0.020
WEIM/LEl	0.51 – 0.56	0.535	0.024	0.010
LP/LEl	0.35 – 0.40	0.372	0.021	0.009
Females				
A. Measurements, in mm.				
LR	2.12 – 2.96	2.565	0.439	0.207
WF	1.32 – 2.00	1.725	0.307	0.145
WRA	1.24 – 1.68	1.510	0.228	0.108
LP	3.12 – 4.56	4.020	0.669	0.315
WPB	3.36 – 4.96	4.290	0.793	0.374
WEIH	4.16 – 6.08	5.250	0.916	0.432
WEIM	4.64 – 6.80	5.760	0.996	0.469
LEl	8.80 –12.48	11.000	1.799	0.848
LEy	1.08 – 1.48	1.325	0.191	0.090
WEy	0.68 – 0.80	0.740	0.079	0.037
B. Proportions				
WEy/LEy	0.52 – 0.63	0.561	0.060	0.028
WPB/LP	1.00 – 1.11	1.066	0.056	0.026
WRA/LR	0.57 – 0.62	0.590	0.024	0.011
WRA/WF	0.84 – 0.94	0.878	0.060	0.028
WEIM/LEl	0.50 – 0.57	0.524	0.030	0.014
LP/LEl	0.35 – 0.39	0.366	0.024	0.011

Table 33. Descriptive statistics for *C. quadrilineatus* based on eight males and eight females from southern Arizona localities

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.84 – 2.36	2.055	0.270	0.127
WF	1.24 – 1.52	1.365	0.185	0.087
WRA	1.16 – 1.48	1.320	0.181	0.086
LP	3.04 – 3.76	3.380	0.434	0.204
WPB	3.28 – 4.08	3.620	0.496	0.234
WElH	3.84 – 5.04	4.360	0.609	0.287
WElM	4.32 – 5.76	4.850	0.714	0.337
LEl	8.48 –10.56	9.500	1.065	0.502
LEy	1.00 – 1.28	1.140	0.128	0.060
WEy	0.60 – 0.76	0.670	0.077	0.036
B. Proportions				
WEy/LEy	0.53 – 0.61	0.588	0.038	0.018
WPB/LP	1.05 – 1.09	1.071	0.022	0.010
WRA/LR	0.60 – 0.67	0.643	0.035	0.017
WRA/WF	0.91 – 1.07	0.968	0.084	0.040
WElM/LEl	0.48 – 0.55	0.510	0.027	0.013
LP/LEl	0.34 – 0.37	0.356	0.014	0.007
Females				
A. Measurements, in mm.				
LR	1.68 – 2.20	1.985	0.353	0.166
WF	1.04 – 1.52	1.325	0.269	0.127
WRA	1.00 – 1.40	1.230	0.207	0.098
LP	2.48 – 3.68	3.250	0.672	0.317
WPB	2.72 – 3.92	3.440	0.670	0.316
WElH	3.20 – 4.88	4.190	0.918	0.433
WElM	3.60 – 5.36	4.670	0.985	0.464
LEl	7.20 –10.40	9.220	1.809	0.853
LEy	0.92 – 1.20	1.110	0.153	0.072
WEy	0.56 – 0.72	0.655	0.084	0.040
B. Proportions				
WEy/LEy	0.55 – 0.64	0.591	0.046	0.022
WPB/LP	1.02 – 1.10	1.060	0.043	0.020
WRA/LR	0.58 – 0.69	0.621	0.050	0.023
WRA/WF	0.84 – 1.00	0.932	0.076	0.036
WElM/LEl	0.49 – 0.52	0.506	0.019	0.009
LP/LEl	0.34 – 0.37	0.352	0.015	0.007

APPENDIX 2

Appendix II: Species of genera of Cleoninae examined for purposes of determining relationships of New World taxa. Genus-group name is listed first, followed by species examined on loan from BMNH. An asterisk indicates that the species examined is the type-species of that generic-group name. No asterisk indicates that the type species was not examined because, no type-species has yet been designated for that genus-group name; or, type species was not available for study in the BMNH.

Adosomus Faust — *A. granulosus* (Mannerheim)
Amblysomus Faust — *A. brevis* (Fåhraeus) *
Ammocleonus Bedel — *A. hieroglyphicus* (Olivier) *
Atactogaster Faust — *A. orientalis* (Chevrolat) *
Bothynoderes Schoenherr — *B. punctiventris* (Germar) *
Brachycleonus Faust — *B. fronto* (Fischer von Waldheim) *
Calodemas Faust — *C. vetustus* Faust
Centrocleonus Chevrolat — *C. fallax* (Fåhraeus) *
Chromoderus Motschulsky — *C. albidus* (Fabricius) *
    [= *C. fasciatus* (Vill.)]
Chromonotus Motschulsky — *C. vittatus* (Hochhuth) *
Chromosomus Motschulsky — *C. fischeri* (Fåhraeus) *
Cnemodontus Chevrolat — *C. limpidus* (Gyllenhal)
Coniocleonus Motschulsky — *C. excoriatus* (Gyllenhal) [type species,
    C. carinirostris (Gyllenhal)]
Conorhynchus Motschulsky — *C. conirostris* (Gebler) *
Cosmogaster Faust — *C. lateralis* (Gyllenhal) *
Cylindropterus Chevrolat — *C. luxeri* Chevrolat *
Cyphocleonus Motschulsky — *C. cenchrus* (Pallas) *
Epirhynchus Schoenherr — *E. humerosus* Faust [type species,
    E. argus (Sparrm.)]
Eumecops Hochhuth — *Eumecops* sp. [type species,
    E. kittaryi Hochhuth]
Eurycleonus Bedel — *E. baluchicus* Marshall [type species,
    E. gigas Mars.]
Gonocleonus Chevrolat — *G. helferi* Chevrolat *
Isomerus Motschulsky — *I. granosus* (Zoubkoff) *
Koenigius Heyd. — *K. palaestinus* Heyd. *
Leucochromus Motschulsky — *L. imperialis* (Zoubkoff) *
Leucomigus Motschulsky — *L. candidatus* (Pallas) *
Leucosomus Motschulsky — *L. opthalmicus* (Rossi) *
Liocleonus Motschulsky — *L. clathratus* (Olivier) *
Lixocleonus Marshall — *L. incanus* Marshall *
Lixomorphus Faust — *L. ocularis* (Fabricius) *
Mecaspis Schoenherr — *M. palmatus* (Olivier)
Menocleonus Faust — *M. implicatus* Faust
Microcleonus Faust — *M. panderi* (Fischer von Waldheim) *
Nemoxenus Faust — *N. zebra* (Chevrolat)
Neocleonus Chevrolat — *N. sannio* (Herbst) *

Nomimonyx Faust   N. perturbans Faust *
Pachycerus Schoenherr   P. cordiger (Germar) [type species,
                                      P. scabrosus Brullé]
Pentatropis Faust   P. sparsus (Fåhraeus) [type species,
                                      P. formosus (Fåhraeus)]
Phaulosomus Faust   P. kilimanus Faust
Pleurocleonus Motchulsky   P. quadrivittatus (Zoubkoff) *
Porocleonus Motschulsky   P. candidus (Olivier) *
Prionorhinus Chevrolat   P. stillatus (Gyllenhal)
Pseudocleonus Chevrolat   P. cinereus (Schrank)
Rhabdorhynchus Motschulsky   R. anchusae Chevrolat [type species,
                                      R. menetriesi (Gyllenhal)]
Stephanocleonus Motschulsky   S. flaviceps (Pallas) *
Temnorhinus Chevrolat   T. brevirostris (Gyllenhal) *
Tetragonothorax Chevrolat   T. retusus (Fabricius) *
Trichocleonus Motschulsky   T. leucophyllus (Fischer von Waldheim) *
Xanthochelus Chevrolat   X. longus Chevrolat *
Xenomacrus Faust   X. glacialis (Herbst)

INDEX TO NAMES OF TAXA
(Synonyms in italics)

SPECIES AND SUBSPECIES

BOOK NOTICES

ENTOMOFAUNAL PUBLICATIONS FROM THE AUSTRALIAN REGION

In recent years, Australian and New Zealand government and museum entomologists have undertaken preparation of major series of faunistic treatments which are of substantial value not only locally but also more distantly, for those extra-territorial biologists who want to gain some level of familiarity with the notogaean arthropod fauna. Previously, *Quaestiones Entomologicae* has published extensive reviews or notices of two series: Fauna of New Zealand, and A Guide to the Genera of Beetles of South Australia. Series previously unnoticed in the pages of *Quaest. Ent.* are the Zoological Catalogue of Australia, and the Fauna of Australia. We have not yet seen any parts of the last named series. Below, comments are offered about recently received parts of the first three series noted.

HARRIS, A. C. 1987. Pompilidae (Insecta: Hymenoptera). Fauna of New Zealand [no.] 12, 154 pp. DSIR Science Information Publishing Centre, P.O. Box 9741, Wellington, New Zealand. Price $39.95 (New Zealand), $34.25 (Canadian).

The 11 species of spider wasps (10 endemic, one introduced from Australia) representing four genera included in two subfamilies, are treated in fulsome manner, including for each species data about: names; structural features of adults and larvae; and way of life, including hunting of spiders by adult females, "nidification formula", nest site and structure, life history, and emergence and copulation. Variation in color and color pattern are clearly indicated by stylized diagrams, and various structural features and nests are illustrated by line drawings and photographs. The frontspiece is a superb photograph of a paralyzed ctenizid spider with a larval pompilid attached.

To aid in identification of taxa, illustrated keys are provided to adults (males and females), larvae, and type of nesting behavior.

An introductory part of the publication treats an appropriately wide variety of biological information about New Zealand pompilids: structural features of adults and larvae, geographical variation, mimicry, nesting behavior, biogeographic relationships, and evolutionary relationships. I found especially interesting the author's observation about mimicry. Three complexes are recognized, based on color pattern of body and wings, and pattern of movement of adults. Each complex has Müllerian and Bastesian components, including collectively, elaterid beetles, asilid and calliphorid flies, ichneumonid, proctotrupid, and sphecid wasps, and bees.

The substantial amount of attention devoted to prey capture and nesting behavior is supplemented by an appendix that records, in association with the name of the predatory wasp species, family, genus and species of the spider prey. Information of this kind will be of interest to general biologists and behaviorists.

Overall, the author has provided a study that easily meets the very high standards associated with publications about aculeate Hymenoptera, in the tradition of such masters as Howard E. Evans, Karl V. Krombein, and Charles D. Michner.

MATTHEWS, E. G. 1987. A guide to the beetles of South Australia. Part 5 Polyphaga: Tenebrionoidea, 67 pp. Special Educational Bulletin Series (No. 8), South Australian Museum, Adelaide, Australia.

This volume, the primary purpose of which is to provide a simplified means of identifying adult beetles to genus, consists principally of illustrated keys and 135 habitus illustrations– some excellent line drawings, and some photographs– one such illustration for each genus. In a chapter preceding the keys, each of the 17 families of tenebrionoids of South Australia is briefly characterized by comparison or by reference to diagnostic structural features, and by reference to way of life. Under each family, genera are listed, and number of species of each genus in South Australia is reported. For the markedly speciose Tenebrionidae (including Alleculidae, Cossyphodidae, Lagriidae, and Nilionidae), the genera are grouped by tribe and subfamily.

The volume is attractively bound with a soft cover, on which is a color illustation of a brownish "pie-dish" tenebrionid of the genus *Helea* on brownish pebbly soil. This useful publication continues the high standard set in the previous volumes in this series.

LAWRENCE, J. F., B. P. MOORE, J. E. PYKE, and T. P. WEIR. 1987. Volume 4 Coleoptera Archostemata, Myxophaga and Adephaga. viii + 444 pp. *In*, Zoological catalogue of Australia (D. W. Walker, Executive Editor). Australian Government Publications Services, Mail Order Sales, G. P. O. Box 84, Canberra A. C. T. 2601. Price $34.95 (Australian), $33.54 (Canadian).

This volume catalogues the taxa of three suborders: Archostemata, including families Cupedidae and Ommatidae, and Myxophaga, family Microsoridae (Lawrence, Weir, and Pyke); Adephaga- Geodephaga, including families Rhysodidae and Carabidae (Moore, Weir, and Pyke); and Adephaga- Hydradephaga, including families Haliplidae, Hygrobiidae, Noteridae, Dytiscidae, and Gyrinidae (Lawrence, Weir, and Pyke).

For taxa of supraspecific rank, arrangement is taxonomic according to the latest revision. For species, arrangement within genera is alphabetical by specific epithet, and within species, subspecies are arranged alphabetically by subspecific epithet.

Information presented for taxa is abundant. For each family, a brief account is given about number of included species, composition, world distribution, fossil record, habits and life cycles, as well as taxonomic history and present state of knowledge of the group within Australia. Generic and specific synonymies are detailed for the Australian components. Data about geographical distribution were compiled from published sources and from personal knowledge of the authors, as appropriate. Habitat and life history data are also included.

Names of taxa in the text are set in boldface, and they stand out clearly. The text is complemented by an extensive index of taxonomic names. The durable volume has hard covers, with a covering of blue cloth.

This contribution is excellent, and is a credit to the authors, editors, and printers, and to the Division of Entomology, CSIRO, under whose aegis the required bibliographical research was carried out. Coleopterists will be looking forward to publication of the remaining parts of this remarkable catalogue that deal with beetles.

George E. Ball

EDITOR'S ACKNOWLEDGEMENTS AND COMMENTS

Reviews of manuscripts were provided by the individuals whose names appear below. The appearance of their names does not imply that the reviewers endorsed the papers published, but only that they helped the Editor, as requested. Their assistance is very much appreciated.

J. S. Ashe
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French translations of abstracts were provided by J. O. Lacoursiere, of my Department. J. S. Scott and D. Shpeley read proof, as required, and assisted in other ways as well.

The Publications Manager, Mrs. S. Subbarao, provided excellent service both in production and management, and thanks to her efforts, some important improvements to our operation will be implemented in the near future.

The staff of Printing Services, University of Alberta, provided generally highly satisfactory issues. This year, a special feature was the color plates in F. A. H. Sperling's treatment of *Papilio machaon* species group. It is a pleasure to acknowledge the careful work of E. Anaka and J. Smith of Printing Services, in printing these plates.

New printing equipment, recently acquired by Printing Services, will provide higher resolution of text and consequent improvement in readability. Eventually, we plan to take full advantage of this improved facility to transfer sophisticated art work. The immediate advantage to authors, of this new equipment, is that they may submit manuscripts on Macintosh discs, using Microsoftword software. Authors who wish to submit manuscripts

generated on other microcomputers should consult the Publications Manager for information.

In an effort to improve the quality of paper, yet control the cost of production, page size will be changed from 6.75 in X 9.75 in. to 6 in. X 9 in. beginning with Volume 24.

George E. Ball